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Roles of biotic and abiotic variables in determining spatial variation of soil respiration in secondary oak and planted pine forests

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A B S T R A C T

Monoculture pine plantation (PP) was widely established after clear-cutting of natural forests last century in China. However, its effects on soil CO_2 efflux (R_S) temporally and spatially are still poorly understood. Biotic and abiotic factors that control spatio-temporal variation of R_S were assessed in a naturally regenerated oak forest (OF) and a nearby PP in a warm temperate area of China. We hypothesized that spatial variation of R_S in PP is lower than that in OF and is less influenced by biotic factors due to its homogeneous stand structure compared to the regenerated OF. R_S measurement campaigns were conducted in two 40 m × 60 m plots in OF and PP from Oct. 2008 to Oct. 2009. Soil temperature at 5 cm depth (T_5) exerted considerable influence on the temporal variation in R_S. However, the spatial variation of R_S was not affected by T_5 in either PP or OF. The observed spatial pattern of R_S remained comparatively consistent throughout the measurement campaigns for both forests. Soil chemical and physical parameters such as soil organic carbon (SOC), light fraction organic carbon (LFOC), total nitrogen (TN), bulk density (BD), total porosity (TP), water-filled pore space (WFPS), and water-holding capacity (WHC) had significant impact on the spatial variation of R_S for both OF and PP. We found that biotic factors such as fine root biomass (FR) and stand structure parameters including basal area (BA), maximum diameter at breast height (max. DBH), and mean DBH within 4–5 m of the measurement points had significant influence on the spatial variation of R_S in OF, while no similar significant correlation was found in PP. A stepwise multi-linear regression showed that water-holding capacity (WHC), max. DBH within 4 m of the measurement points (max. DBH_4), and total porosity (TP) contributed 68.7% to the spatial variation of R_S in OF, while light fraction organic carbon (LFOC) and bulk density (BD) accounted for 46.9% of the spatial variation of R_S in PP. These differentiated the importance of biotic and abiotic factors in controlling the spatial variation of R_S between the naturally regenerated OF and the artificially regenerated monoculture PP. Therefore, compared to OF, relatively lower coefficients of spatial variation for R_S were observed in PP across the year, which was partly attributed to its simple stand structure of PP. Our findings are valuable for accurately estimating regional carbon fluxes by considering the spatio-temporal variation of R_S in artificially and naturally regenerated forests.

1. Introduction

Soil CO_2 efflux (R_S) is the second largest terrestrial carbon flux and is sensitive to climate, vegetation type, as well as soil properties (Raich and Potter, 1995; IPCC, 2001; Palmroth et al., 2005). Soil temperature and soil water content (SWC) are recognized as the main factors in controlling the temporal variability of R_S (Davidson et al., 1998; Janssens et al., 2001). However, spatial variability of R_S has not been well understood due to its complex component origin (Søe and Buchmann, 2005) as both autotrophic and heterotrophic organisms contribute to soil-surface CO_2 efflux through respiration (Boone et al., 1998; Hanson et al., 2000). Therefore, biotic and abiotic factors related to autotrophic and heterotrophic respiration will inevitably affect R_S spatially. Factors such as spatial distribution of fine roots and their turnover rate (Saiz et al., 2006; Tang et al., 2009), plant photosynthesis (Tang et al., 2005), leaf area and primary productivity (Högberg et al., 2001; Rey et al., 2002; Yuste et al., 2004), allocation patterns of recent photosynthates to roots (Högberg et al., 2001; Bhupinderpal-singh et al., 2003), and stand structure (Søe and

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Buchmann, 2005; Katayama et al., 2009) all contribute to variation in autotrophic respiration. On the other hand, heterotrophic respiration is mainly controlled by soil biophysical environments and substrate availability; e.g. aboveground and belowground litter fall (Ryan and Law, 2005), soil organic carbon (SOC) (Xu and Qi, 2001b; Wang and Yang, 2007) or labile SOC (Laik et al., 2009), nitrogen, phosphorus, and magnesium (Xu and Qi, 2001b; Søe and Buchmann, 2005; Ohashi and Gyokusen, 2007). In addition, soil physical characters such as bulk density (BD), porosity, and water-filled pore space (WFPS) also determine the spatial pattern of soil respiration by affecting gas diffusivity (Jassal et al., 2004; Søe and Buchmann, 2005; Ullah et al., 2008; Lin et al., 2009). Thus, factors ranging from soil chemistry and physics to stand structure and root distribution may explain the spatial variation of soil respiration. Furthermore, spatial patterns of soil respiration may vary with time because of changes in controlling factors (Xu and Qi, 2001b). Therefore, determining factors affecting the spatial variation in soil respiration is crucial not only for understanding CO_2 dynamics but also for accurately estimating total forest R_S (Katayama et al., 2009).

The difference in magnitude of R_S among different forest types may have a large effect on the net ecosystem exchange (NEE) of the forests and may also show different responses to future climate change (Palmroth et al., 2005). In China, warm temperate forests account for a large proportion of the nation's total forested area, which are a mosaic composed largely of pine plantations (PPs) and naturally regenerated hardwood forests. Artificially regenerated forests, which are always monoculture PPs, have simplified stand structure compared to naturally regenerated forests. Moreover, due to long-term differences in the quantity and quality of litter input (needle or broad leaf), soil organic matter quality may also be different in these two forests (Li et al., 2005; Luan et al., 2010). Therefore, the belowground carbon dynamics would be changed substantially and thus lead to different soil-surface CO_2 efflux patterns. Nevertheless, no studies have been conducted in this area so far to elucidate the mechanisms of spatio-temporal variations in R_S of these two forest types, which are critical for estimating current and future C budgets for this region. To accomplish this, we compared CO_2 efflux in a PP and a nearby OF which were, respectively, artificially and naturally regenerated from a harvest site ca. 50-years ago with similar site history and soil conditions. We hypothesized that biotic and abiotic factors would differently influence the spatial variation of soil respiration between these two forests. The specific objectives of this study were to (1) identify the spatio-temporal variation of soil respiration in a naturally regenerated OF and a nearby PP in a warm temperate area of China; and to (2) evaluate factors that affecting spatial variability of soil respiration in these two forests.

2. Materials and methods

2.1. Study sites and experimental design

The study sites were located at the Forest Ecological Research Station in the Baotianman Natural Reserve (111°47′–112°04′E, 33°20′–33°36′N), Henan Province, China. The average elevation is 1400 m. The meteorological parameters were collected from a nearby weather station less than 3 km away from the study site. The annual mean precipitation and air temperature were 900 mm and 15.1 °C, respectively. Precipitation occurred mainly in Summer (June–August, 55–62%; Liu et al., 1998). Upland soils were dominated by mountain yellow brown soil (Chinese classification). The OF stand was dominated by *Quercus aliena* var. *acuteserrata*, with some old residual trees located randomly in the plot. In addition to the dominant species, other tree species including *Carpinus cordata* Bl., *Cornus controversa* Hemsl., *Tilia americana*, and *Carpinus turczaninowii* Hance have also been discovered in the plot. In the PP stand, *Pinus armandii* F. was the dominant canopy species, along with some *Q. aliena* var. *acuteserrata*. The sub-canopy contained 22 woody species, of which *Dendrobenthamia japonica* var. *chinensis* Fang, *Lindera obtusiloba* Bl., *C. cordata* Bl., and *C. turczaninowii* Hance were the most prevalent. No intensive management has been carried out in the PP since its establishment. Two 40 m × 60 m study plots were established in each stand with an average slope of <8°. A 10 m × 10 m square grid was then placed within each plot and 35 subplots (1 m × 1 m) were positioned at each intersection.

2.2. Soil respiration and microclimate

We measured soil respiration (R_S) from October 2008 to October 2009 using a Li-8100 soil CO_2 flux system (LI-COR Inc., Lincoln, NE, USA) for a total of 12 (OF) and 13 (PP) measurement campaigns. PVC measurement collars (19.6 cm inside diameter) were installed at each subplot in September 2008. All collars were left at the site throughout the study period. Two measurement cycles (3 min for each cycle) were carried out at each location and the mean was used to calculate the soil CO_2 efflux. Soil temperature at 5 cm (T_5) was measured adjacent to each respiration collar with a portable temperature probe provided with the Li-8100. Soil volumetric water content (SWC) at 0–5 cm was measured with a portable time domain reflectometer MPKit-B soil moisture gauge (NTZT Inc., Nantong, China) at three points close to each collar for each R_S measurement. No rainfall occurred during the actual observations at each plot. We also avoided early morning and post-rain measurements to prevent rapid transition of the soil respiration rate during observations.

2.3. Soil physical and chemical properties, root and stand structure features

Five soil samples were collected from the top 5 cm of the mineral soil next to each collar using 100-ml (50.46 mm diameter, 50 mm height) sampling cylinders in August, 2009. We mixed three soil samples for mass-based soil organic carbon (SOC), nitrogen content (TN), and light fraction organic carbon (LFOC) measurement. The remaining two samples were used for analyses of bulk density (BD), water-holding capacity (WHC), and total soil porosity (TP) based on soil water-retention characteristics (Liu et al., 2009). Light-fraction soil organic matter at a depth of 0–10 cm was obtained by density fractionation based on a study by Six et al. (1998), but with a modification using $CaCl_2$ solution (density of 1.5 g ml^{-1}; Garten et al., 1999). Bulk-soil and light fraction organic carbon contents were determined by the wet oxidation method with 133 mM $K_2Cr_2O_7$ at 170–180 °C (Lu, 2000). Roots were extracted from two fresh soil cores (0–30 cm depth, 10 cm diameter) located within c. 1 m of the centre of the respiration collars in August, 2009. The samples were washed and grouped into coarse (>5 mm), medium (2–5 mm), and fine (<2 mm) roots. They were manually separated and the dry biomass (70 °C, 24 h) was recorded correspondingly. In August 2009, the diameter at breast height (DBH) and the location of each tree with a DBH greater than 1 cm was measured in each plot. From these data, we calculated structure parameters such as total basal area (BA_r), maximum DBH (max. DBH_r), and mean DBH (mean DBH_r) for trees within 2–10 m (radius) of the measurement points. The leaf area index (LAI) was measured above each subplot using hemispherical photographs with WinSCANOPY (Regent Instruments Inc., Quebec, Canada) in August 2009. Water-filled pore space (WFPS) was calculated as follows:

$$\mathrm{WFPS} = \frac{\mathrm{SWC}}{1 - \frac{\mathrm{BD}}{\mathrm{PD}}} \quad (1)$$