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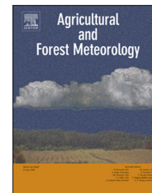

Microbial properties regulate spatial variation in the differences in heterotrophic respiration and its temperature sensitivity between primary and secondary forests from tropical to cold-temperate zones

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ABSTRACT

Large quantities of forest products globally have been lumbered, resulting in widespread conversion from primary forests [PFs] to secondary forests [SFs]. This transformation has exerted important impacts on the global carbon [C] cycle. Therefore, it is essential to clarify how soil C, which is a vital component of the global C pool, responds to the converting of forests from PFs to SFs, in parallel to identifying the underlying mechanisms. Here, nine paired (PFs and SFs) soil samples (0–10 cm) were obtained from tropical to cold-temperate zones along the north-south transect of eastern China (NSTEC). The heterotrophic respiration rate [R_H] as per soil organic C at a reference temperature of 20 °C [$R_{20\text{-}C}$] and its temperature sensitivity [Q_{10}] were measured and calculated through 14 d incubation experiments. Our results showed that most of $R_{20\text{-}C}$ and Q_{10} in SFs were greater than those in PFs. Strong spatial variation in the differences in $R_{20\text{-}C}$ and Q_{10} between PFs and SFs [$\triangle R_{20\text{-}C}$, $\triangle Q_{10}$] was observed along the NSTEC, with the greatest $\triangle R_{20\text{-}C}$, $\triangle Q_{10}$ being detected in the soils of mid-latitude forests. Overall, 83.2% of the spatial variation in $\triangle R_{20\text{-}C}$ was explained by physical-chemical and microbial properties, which contributed 68.5% and 52.4% variation solely, respectively. Similarly, 79% of the variation in $\triangle Q_{10}$ between PFs and SFs was explained by microbial properties, physical-chemical properties, and dissolved organic C, which contributed 81.6%, 10.5%, and 9% variation solely, respectively. Overall, our findings demonstrate high spatial variation in $\triangle R_H$ and $\triangle Q_{10}$ between PFs and SFs, which was mainly explained by microbial properties of soils.

1. Introduction

Forest ecosystems exchange energy, water, nutrients and, in particular, carbon [C] with the surrounding environment, and play major roles in the global C cycle. For instance, forests store large quantities of soil organic carbon [SOC] with high productivity (Battle et al., 2000; Goodale et al., 2002; Fang et al., 2007; He et al., 2017). Soil respiration [R_S] releases as much as half the total CO_2 production (Schlesinger and Andrews, 2000), most of which is produced by the activity of heterotrophic microorganisms [R_H] (Pries et al., 2017).

However, R_S in forest ecosystems is sensitive to changes in the climate and vegetation type, especially forest degradation, such as that primary forests [PFs] are converted to secondary forests [SFs] (Medlyn et al., 2005; Anderson-Teixeira et al., 2016). For example, SFs in the Amazon release more C (with *ca.* 1.3 Pg C yr^{-1}) than PFs (Espirito-Santo et al., 2014). However, Sheng et al. (2010) reported that the annual accumulation of R_S was reduced by 32% after converting PFs to SFs in a subtropical region. That is, converting PFs to SFs plays an important role to the global C pool, with controversy existing over how it influences the balance of C stocks. Because of human interventions associated with forest management and silviculture, two thirds of global PFs have been converted to SFs (FAO, 2006; Lungo et al., 2006), leading to a significant decrease in the soil C pool based on global meta-analysis (Don et al., 2011; Zhou et al., 2018). Therefore, it is important to clarify the mechanism leading to differences in Rs [$\triangle Rs$] as a result of converting PFs to SFs.

Based on existed researches, three properties could potentially explain spatial variation in $\triangle R_S$: microbial, substrate, and soil physical-

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chemical properties (Adachi et al., 2006; Zhang et al., 2016; Buchkowski et al., 2017). Usually, microbial properties included community composition, biomass, and activities of enzymes for C decomposition. Different microbes showed different preferences to soil organic matter [SOM]; for instance, bacteria prefer labile SOM, while fungi prefer recalcitrant SOM (Lehmann and Kleber, 2015). Thus, this difference in *R*s might due to the various extracellular enzymes produced by microbes (Dungait et al., 2012; Ali et al., 2018). Previous studies reported that soil microbial biomass dominates the amount of enzymes present (Bååth, 1998; Fritze et al., 2000). Besides, enzyme activity might be regulated by pH (Min et al., 2014) and electricity conductivity (Iwai et al., 2012), which primarily influence microbial biomass. In addition to these physical-chemical properties, the growth of microorganisms could be significantly accelerated when available substrate is abundant, whereas an increase in the growth of microbes might result in a decrease in available substrate. That is, there existed an interaction effect between microbes and substrate to influence *R*s. In particular, SOM quality might change the temperature sensitivity [Q_{10}] of *R*s, which is closely related to the "Carbon quality –temperature sensitivity" hypothesis (Bosatta and Ågren, 1999). That is, substrates of low quality require higher energy for microbes to degrade, leading microbes to exhibit higher sensitivity to warming than they would in substrates of high quality (Gershenson et al., 2009; He et al., 2013; Wang et al., 2016b).

Nevertheless, previous studies generally focused on single research sites, making it difficult to obtain a general pattern and elucidate the underlying mechanisms driving $\triangle R_S$, particularly in China (Sheng et al., 2010; Liu et al., 2011; Shi et al., 2015). Forests in China extend across most of forest types in the Northern Hemisphere (18.74–53 °N) and exhibit a significant hydrothermal gradient (Zhang and Yang, 1995). Due to the rapid growth in the economy and increased demand for timber and food production, deforestation increased at a sharp rate in China during the second half of the 20th century, resulting in a large amount of PFs being converted to SFs (Shi et al., 2009). Therefore, understanding the pattern of $\triangle R_S$ in China might help us to elucidate how forest degradation affects soil C stocks at regional or global scales.

In this study, we collected nine paired (PFs *vs.* SFs) surface (0–10 cm) forest soils along the north-south transect of eastern China [NSTEC]. Then, we conducted a 14-d incubation experiment to investigate differences in heterotrophic respiration rate (per soil organic C at a reference temperature of 20 °C [$R_{20\text{-C}}$]) and Q_{10} between PFs and SFs ($\triangle R_{20\text{-C}}$, $\triangle Q_{10}$), along with differences in the background values of potential explanatory factors (physical-chemical *vs.* substrate *vs.* microbial properties). We aimed to clarify: 1) whether R_H in SFs are consistently higher than that in PFs; 2) whether a clear spatial trend in $\triangle R_H$ ($\triangle R_{20\text{-C}}$, $\triangle Q_{10}$) exists from tropical to cold-temperate zone; and 3) what factors dominate the spatial variation in $\triangle R_H$ ($\triangle R_{20\text{-C}}$, $\triangle Q_{10}$)?

2. Materials and methods

2.1. Sites description and pre-treatment

The NSTEC (108.86°–123.29 °W, 18.74°–51.76 °N) is a unique forest belt (Fig. 1) that has a significant thermal gradient (Zhang and Yang, 1995; Zhao et al., 2016) from north to south. The mean annual temperature ranges from –3.67 °C to 23.15 °C and the mean annual precipitation ranges from 473 mm to 2266 mm (Table 1). Nine coupled forests with relatively homogenous and representative vegetation were selected along the NSTEC. They were designated as cold-temperate coniferous forest (site: Huzhong), temperate *Pinus koraiensis*-broadleaf mixed forest (Liangshui and Changbai), warm temperate deciduous broad-leaved forest (Dongling and Taiyue), north subtropical evergreen and deciduous broad-leaved mixed forest (Shennong), subtropical evergreen broad-leaved forest (Jiulian), south subtropical evergreen broadleaved forest (Dinghu), and tropical mountain rain forest (Jianfeng), respectively (Fig. 1, Table 1) (Tian et al., 2016a; Wang et al., 2016c). PFs were either long-term experimental sites or sites selected from natural protected areas in China, to exclude any strong human disturbance over the last five decades. SFs were located adjacent to PFs and had similar topography and slope with secondary succession following lumber harvesting.

Field sampling was conducted from July to August. We set up four 30 m × 40 m plots in each forest (He et al., 2018). Soil surface samples (0–10 cm) were collected from four randomly chosen locations in each plot and were combined to form one composite sample for per plot (Wang et al., 2016b; Xu et al., 2017). Soil samples were sieved (< 2 mm diameter), with all roots and visible organic debris being removed manually. For each forest, homogenized soils were divided into three subsamples: (1) froze at −80 °C to measure soil microbial properties, including enzyme activities and microbial community, (2) to measure soil biochemical and physical properties, and (3) stored at 4 °C before incubation experiments.

2.2. Analysis of soil physical-chemical and substrate properties

In this study, soil physical-chemical properties included soil pH, oxidation-reduction potential [ORP], conductivity [COND], bulk density [BD], and soil texture (Table S1). pH, oxidation-reduction potential, and conductivity were measured by "Ultrameter II" (Myron L Company, USA) (slurry of soil and ultrapure water, 1:2.5). Particle size distribution was determined using the Mastersizer 2000 (Malvern, UK) laser diffractometer (Sochan et al., 2012), and was further classified into clay (< 2 μm), silt (2–50 μm) and sand (50–2000 μm) based on the soil texture classification system of American.

Soil water content was measured using the methods of oven-dried and weighted. Soil water holding capacity was determined by rewetting it for 12 h, followed by draining it through filter paper for 12 h. Soil water content was calculated by the soil samples that were weighed before and after over-drying at 105 °C for 24 h (Wang et al., 2016b).

We measured four substrate properties, *i.e.*, the contents of SOC, total nitrogen [TN], dissolved organic carbon [DOC], and dissolved total nitrogen [DTN] (Table S2). The contents of SOC and TN were measured using an elemental analyzer (Elementar, Vario Max, Germany). DOC and DTN were measured using the non-fumigated samples (one part of chloroform-fumigation for microbial biomass) with a total organic carbon instrument (liquid TOC II, USA) and continuous flow analyzer (Futura, France), respectively.

2.3. Analysis of soil microbial properties

To assess how microbial properties affect $\triangle R_H$, we selected the microbial biomass, community structural, and enzymes related to C decomposition (Table S3). The chloroform-fumigation method was used to estimate microbial biomass, including microbial biomass C [MBC] (1/Kc = 2.22, Baumann et al., 1996) and microbial biomass nitrogen [MBN] (1/Kn = 1.85, Brookes et al., 1985), with 0.5 M K_2SO_4 (slurry of soil and K_2SO_4 solution, 1:5). The leach liquor was measured with a total organic C instrument (liquid TOC II; USA) and continuous flow analyzer (Futura, France), respectively (Wang et al., 2016b). Phospholipid fatty acid content was measured to obtain the microbial community structural using the mild alkaline methyl esterification method and gas chromatography and mass spectrometry (Thermo ISQ TRACE GC system Ultra ISQ, Germany) (Xu et al., 2015). Based on the results of phospholipid fatty acid and the rules of Frostegard and Bååth (1996), bacteria, fungi, actinomyces were classified as three different microbial communities.

The enzymes related to C decomposition selected in this study were based on previous studies (Xu et al., 2015; Min et al., 2014), and included β-D-glucosidase [βG, representing the terminal reaction in cellulose degradation], *N*-acetyl-β-D-glucosidase [NAG, representing hydrolyzes leucine and other hydrophobic amino acids from the N-

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