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Biochar reduces soil heterotrophic respiration in a subtropical plantation through increasing soil organic carbon recalcitrancy and decreasing carbon-degrading microbial activity

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ABSTRACT

Carbon (C) storage in forest soils can be enhanced through increasing organic C input and decreasing soil heterotrophic respiration (R_H). The inhibitory effect of biochar on R_H has been extensively studied in agricultural soils, while such an effect and the mechanisms involved remain unknown in forest soils. Here, we examine the response of soil physicochemical and microbial properties to biochar application and how these factors mediate the biochar-induced change in soil R_H in a subtropical bamboo plantation. Our results showed that biochar application significantly reduced R_H, and markedly altered most of the studied soil properties important for R_H in the bamboo plantation. Biochar application did not affect soil temperature and no relationship between soil R_H and either soil moisture or labile organic C content was observed, excluding the possibility that biochar reduced the R_H through changing soil temperature, moisture or labile organic C content, factors commonly considered to control R_H. As compared to the control, biochar application significantly increased the aromatic C content and RubisCO enzyme activity, while decreased β-glucosidase and cellobiohydrolase (CBH) activities. In addition, the soil R_H was positively ($P < 0.01$) correlated with β-glucosidase and CBH activities, while negatively ($P < 0.05$) correlated with RubisCO enzyme activity. Further, using structural equation modelling, we revealed that bicohar reduced R_H through increasing the proportion of soil recalcitrant C fraction and decreasing the β-glucosidase and CBH activities in relation to the decomposition of carbohydrates and celluloses in the soil. This is the first report that increased soil organic C recalcitrancy and decreased activities of C-degrading enzymes are responsible for biochar to reduce R_H in the subtropical plantation, which may be key to regulating R_H in subtropical plantations through forest management.

1. Introduction

The global soil organic carbon (SOC) stock is larger than the sum of atmospheric C and plant biomass C (Lehmann and Kleber, 2015), and the SOC stored in forests accounts for about 70% of the global SOC (Jandl et al., 2007), suggesting that changes in the SOC stock in forests could considerably influence the atmospheric CO_2 concentration (Peng et al., 2008). Soil respiration (R_S) is the main pathway of C efflux from the soil to the atmosphere that has an annual rate of 68–79 Pg CO_2-C globally (Raich and Potter, 1995; Xu and Shang, 2016). The R_S consists of autotrophic respiration (R_A) and heterotrophic respiration (R_H), with R_A originating from root and rhizosphere respiration, and R_H from microbial decomposition of soil organic matter (SOM) (Baggs, 2006; Hopkins et al., 2013). The change in R_A has little effect on the variation in the SOC stock (Kuzyakov, 2006), while the change in R_H could substantially alter the pool size of SOC and the atmospheric CO_2

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concentration (Moinet et al., 2016). Thus, it is critically important to regulate the rate of R_H for forecasting future changes in SOC stock and mitigation of global climate change (Wang et al., 2010; Moinet et al., 2016).

Elucidating the mechanisms that affect soil R_H is critical for developing methods to manage R_H. The rate of soil R_H greatly depends on soil microbial activity and substrate availability, since it is derived from the microbial decomposition of SOM and plant residue (Zhou et al., 2012; Whitaker et al., 2014; Ding et al., 2016). Soil temperature and moisture have been considered as vital factors that control R_H through directly affecting soil microbial activity and indirectly changing the substrate availability (Davidson et al., 2006; Wan et al., 2007). Although soil temperature and moisture content can account for a considerable proportion of the variation in R_H (Li et al., 2010; Moyano et al., 2013; Matteucci et al., 2015), a large proportion of the variation has not been fully understood.

Soil microorganisms generally play a vital role in the decomposition of SOM. The microbial mechanisms involved in regulating R_H, however, has rarely been thoroughly investigated (Cleveland et al., 2007; Schmidt et al., 2011; Chen et al., 2017b). Neither soil microbial biomass nor the microbial community composition determined by phospholipid fatty acids (PLFAs) accounted for the variation of R_H across four subtropical forests (Wei et al., 2015). Changes in R_H have been linked to soil bacterial community composition using PCR-based methods (Cleveland et al., 2007; Fierer et al., 2007). The decomposition or transformation of SOM is also affected by the activities of extracellular enzymes such as β-glucosidase (Chen et al., 2013; Ge et al., 2017), cellobiohydrolase (CBH) (Zhang et al., 2017b) and RubisCO enzyme (Guo et al., 2015). While field evidence on the relationship between R_H and C-cycling enzyme activities is still scarce (Zhou et al., 2012; Xue et al., 2016). In addition, the positive relationship between substrate availability and R_H has mostly been studied in laboratory experiments (Wild et al., 2014), with the relationship seldom tested in field studies. Moreover, substrate availability may also indirectly affect the R_H through altering the soil microbial community composition (de Graaff et al., 2010; Thiessen et al., 2013; Ma et al., 2016). However, there has been no field study to comprehensively evaluate relationships among R_H and soil substrate availability, microbial community composition, and the activities of C-cycling enzymes.

Increasing organic C input to the soil or decreasing SOM decomposition are effective ways to increase soil C stock (Paustian et al., 2016). Addition of biochar derived from plant biomass not only can reduce pollutant (heavy metals and organic pollutants) concentrations in soils (Inyang et al., 2016; Igalavithana et al., 2017; Thangarajan et al., 2018), but can also increase soil C sequestration due to their high resistance to decomposition (Baldock and Smernik, 2002; Lehmann and Joseph, 2015; Li et al., 2018), and therefore has been used as a management strategy to mitigate global climate change (Cox et al., 2000; Zimmerman et al., 2011; Zhou et al., 2017; Zhang et al., 2017a; Bamminger et al., 2018). Biochar application strongly influences both the composition of and substrate availability to soil microbial communities (Steinbeiss et al., 2009; Zimmerman, 2010; Khodadad et al., 2011; Luo et al., 2013), which jointly control the decomposition of native SOC and ultimately affect R_H (Zimmerman et al., 2011; Lu et al., 2014; Zhou et al., 2017). Owning to the broad impact on various soil properties by biochar application (Igalavithana et al., 2017), significant gaps remain in our current understanding of how soil R_H respond to biochar-induced changes in SOC bioavailability, microbial community composition and function, and their interactions. Such gaps would cause large uncertainties regarding how to develop policy-relevant quantitative measures in relation to biochar addition and expected C sequestration (Schmidt et al., 2011).

Forest plantations in China account for about one third of the global area of plantation and contributed about 80% of the total forest C sink increment in China (FAO, 2010; Fang et al., 2014). Recently, some studies have revealed that management practices such as fertilization and understory removal would markedly decrease SOC stock and increase R_S (Liu et al., 2011; Li et al., 2013, 2014; Vogel et al., 2015), which negatively affects C sequestration in forest soils. Therefore, it is of great significance to develop forest management practices that can increase SOC stock but decrease R_H. Application of biochar produced by forest-origin residues has been regarded as an economical and environmentally sustainable strategy for C sequestration (Jeffery et al., 2015). The inhibitory effect of biochar on SOM decomposition or R_H in agricultural soils has been tested through laboratory incubation experiments (Lu et al., 2014; Chen et al., 2017a), while such an effect and the mechanisms involved are poorly understood in forest soils (Li et al., 2018).

Bamboo is widely distributed in subtropical and tropical regions, accounting for approximately 0.8% of the global total forest area in 2010 (FAO, 2010). Among the bamboo species, the Moso bamboo (*Phyllostachys edulis*) has a global area of 4.2 million ha and is the most abundant bamboo species (Yan et al., 2015; Yuen et al., 2017). Moso bamboo is a fast-growing forest species with a great potential of fixing CO_2 from the atmosphere and provides substantial economic and ecological benefits in the Asia-Pacific region (Yuen et al., 2017; Hu et al., 2018). Here, we investigate the response of soil physicochemical and microbial properties to biochar application and how these factors mediate biochar-induced changes in soil R_H in a subtropical Moso bamboo plantation. The specific objectives of this study were (i) to investigate the effects of biochar application on the soil R_H and the soil physicochemical and microbial properties important for R_H in the bamboo plantation and (ii) to elucidate the mechanisms for the biochar-induced changes in soil R_H in the bamboo plantation.

2. Materials and methods

2.1. Experimental site

The research was carried out at an experimental site in Shankou Township (30°14′N, 119°42′E), Hangzhou City, China. The site is in a hilly area with an elevation of ∼150 m. The climate is subtropical with a mean annual temperature of 15.8 °C, and1946 h of sunshine and 239 frost-free days per year. The monthly average air temperature and monthly cumulative precipitation during the study (from September 2015 to September 2016) are presented in Fig. S1. The soil is a Ferralsol according to the FAO soil classification system (WRB, 2006). We selected an 1500 m^2 area to establish the experiment in December, 2014. The Moso bamboo plantation in the study site was converted from a natural evergreen broadleaf forest by planting bamboo after harvesting the broadleaf forest. The Moso bamboo plantation in this study was 16 years old in 2014. The mean diameter at breast height of the studied bamboo plantation was 9.9 cm, with a stocking density of 2880 culm ha^{-1} when measured at the beginning of this study in 2014. In June of each year, fertilizers including urea (200 kg N ha^{-1}), super phosphate (60 kg P ha^{-1}), and potassium chloride (70 kg K ha^{-1}) were broadcast applied, followed by deep tillage to 30–35 cm depth. During the experimental period, no fertilizer was applied in the plots. The ground vegetation in the study plots was manually removed annually. The experimental area was divided into 3 blocks, and soil samples were taken from the 0–20 cm depth from five randomly selected points in each block with a corer. The five soil samples collected from each block were mixed to form a composite sample for each block. The average values for the selective physicochemical properties (see methods described below) in this site were: pH of 4.48, bulk density of 1.14 g cm^{-3}, organic C of 18.6 g kg^{-1}, total N of 2.14 g kg^{-1}, available P of 9.98 mg kg^{-1}, available K of 99.3 mg kg^{-1}, sand of 354 g kg^{-1}, silt of 382 g kg^{-1}, and clay of 264 g kg^{-1}.

2.2. Experimental design

The experiment included three treatments with four replications.