



Linking soil fungal community structure and function to soil organic carbon chemical composition in intensively managed subtropical bamboo forests



Yongchun Li ^{a, b}, Yongfu Li ^{a, b, *}, Scott X. Chang ^c, Xue Liang ^b, Hua Qin ^{a, b}, Junhui Chen ^b, Qiufang Xu ^{a, b, **}

^a The Nurturing Station for the State Key Laboratory of Subtropical Silviculture, Zhejiang A & F University, Lin'an 311300, China

^b Zhejiang Provincial Key Laboratory of Carbon Cycling in Forest Ecosystems and Carbon Sequestration, Zhejiang A & F University, Lin'an 311300, China

^c Department of Renewable Resources, University of Alberta, 442 Earth Sciences Building, Edmonton AB T6G 2E3, Canada

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ABSTRACT

Intensive forest management practices such as organic mulching and heavy fertilization can affect soil microbial composition and function, and soil organic carbon (SOC) forms. However, the linkage between soil microbial community composition and SOC forms is poorly understood in bamboo (*Phyllostachys praecox*) plantations under intensive management (mulching and fertilization). We examined the relationship between SOC (solid state ¹³C NMR) and fungal community compositions (real-time PCR, terminal restriction fragment length polymorphism, and clone library) in a chronosequence of intensively managed bamboo plantations (0, 1, 6, 10, and 15 years of stand age). The fungal community composition (internal transcribed spacer, ITS) and function (cellobiohydrolases, *cbhl*) and C forms in the top- (0–20) and subsoils (20–40 cm) were determined as fungi dominate cellulose (the main component of plant residues) decomposition in the soil. Soil fungal abundance (copy number of 18S rRNA) was positively correlated to O-alkyl C and aromatic C while negatively correlated to alkyl-C and carbonyl C concentrations. The alkyl C was the most influential SOC fraction on fungal community composition before intensive plantation management was applied, while O-alkyl C was the most influential C-form after more than 5 years of intensive management. The alkyl C, O-alkyl C, aromatic C and carbonyl C together explained 63.2 and 54.2% of the variations in total fungal composition in the top- and subsoils, respectively. Saprotrophic or cellulose-degrading species, mainly *Mortierellales* sp., *Trichoderma* sp. and *Scheffersomyces* sp., dominated the fungal community and the dominance increased with increasing plantation age (combined effects of stand age and duration of intensive management). The increased O-alkyl C concentration caused by increased plantation age explained shifts in the *cbhl*-containing community composition. Both the *cbhl* abundance and readily oxidizable C concentration increased with increasing plantation age in the topsoil but not in the subsoil. We conclude that in the intensively managed bamboo plantations changes in organic C forms were closely linked to changes in soil fungal community composition; such linkages have implications for soil nutrient cycling and C transformation in the plantation ecosystem.

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* Corresponding author. The Nurturing Station for the State Key Laboratory of Subtropical Silviculture, Zhejiang A & F University, Lin'an 311300, China.

** Corresponding author. The Nurturing Station for the State Key Laboratory of Subtropical Silviculture, Zhejiang A & F University, Lin'an 311300, China.

E-mail addresses: yongfuli@zafu.edu.cn (Y. Li), xuqiufang@zafu.edu.cn (Q. Xu).

1. Introduction

Forest plantations play a vital role in supporting the timber industry, increasing the development of the local economy and mitigating global climate change (FAO, 2007). To meet the increasing demands for more forest products and greater economic return, native forests and even some agricultural lands have increasingly been converted to intensively managed plantations

(Wu et al., 2010; Eclesia et al., 2012). Intensive forest management practices such as mulching, fertilizer application and tillage could markedly change the quantity and chemical quality of the soil organic C (SOC) (Huang et al., 2008; Zhang et al., 2009), and consequently alter soil microbial characteristics (Xu et al., 2008; Qin et al., 2014). Lei bamboo (*Phyllostachys praecox*), for example, is intensively managed through organic mulching and heavy fertilization to stimulate early bamboo shoot emergence and increase the total production of bamboo shoots, which are harvested and used as a popular healthy food (Jiang et al., 2006). These intensive management practices have resulted in not only shifts in the chemical composition of SOC, mainly including increased alkyl C and decreased aromatic C contents (Li et al., 2010), but also decreases in soil microbial biomass C (MBC), microbial activity, and the diversity of C sources utilized by microbial communities (Xu et al., 2008). However, the linkage between SOC forms and soil microbial community composition has been poorly understood, especially in forest plantations under intensive management.

Soil fungi represent a major part of the microbial population and predominant decomposers of soil organic matter (SOM) (Lodge, 1993; Miura et al., 2013). Fungi typically dominate the degradation of the polymerized fraction of litter such as cellulose and lignin (Poll et al., 2008; Fontaine et al., 2011). However, results regarding the potential role of fungi in the degradation of recalcitrant C forms have been inconsistent (Ng et al., 2014; Wang et al., 2015). For example, Ng et al. (2014) found that marginal differences in aromatic C content led to a very different fungal PLFA (phospholipid fatty acids) marker 18:2w6,9 content in two contrasting agricultural soils, while Wang et al. (2015) reported that soil fungal PLFAs were not correlated with the alkyl C concentration in subtropical plantation soils under four different tree species. It remains uncertain whether soil fungal community shifts in response to changes in SOC composition and chemical quality in intensively managed plantations.

It has been suggested that C accumulation may be more tightly coupled to microbial decomposition processes than to organic C input, since the practice of organic C input did not necessarily result in increased SOC storage (Fan et al., 2012). In the soil, the decomposition of cellulose is especially important in the overall decomposition of SOM, since cellulose is the most abundant polysaccharide in plant litter (Štursová et al., 2012). The *cbhl* gene encodes fungal cellobiohydrolase (CBH), and its gene product catalyses the rate-limiting step in the decomposition of cellulose (Baldrian and Valášková, 2008; Edwards et al., 2008). The diversity and community structure of the *cbhl* gene showed significant correlations with the CBH activity (Fan et al., 2012), which in turn has been linked to altered rates of decomposition in the soil (Allison and Vitousek, 2004). Therefore, targeted analysis of the *cbhl* gene could provide insights into C cycling driven by fungi (Mueller et al., 2014). The *O*-alkyl C (cellulose residue) can dominate the SOC in intensively managed bamboo forests (Li et al., 2010). Marschner et al. (2003) found that intensive management (mainly including organic and inorganic fertilizer applications) affected fungal community composition as well as SOM decomposition. The question remains as to what extent increased cellulose residue input or *O*-alkyl C content influences the population size and composition of the *cbhl*-containing community in intensively managed plantations.

More than 50% of the soil C stock is found in the subsoil (below 20–30 cm) in most agricultural and forest ecosystems (Batjes, 1996; Salome et al., 2010), and subsoil C was found to respond to land-use and/or management changes (Wright et al., 2007; Follett et al., 2009). The intensive management of bamboo forests has been found to increase the *O*-alkyl C (carbohydrates, cellulose and hemicellulose) content both in the top- and subsoils, but decrease

aromatic C (lignin and aromatic compounds) content in the subsoil (Li et al., 2010; Zhang et al., 2013). The chemical nature of organic compounds largely controls the intensity of decomposer activities and rates of degradation (Fontaine et al., 2007). Fungal communities are thought to be an important part of C cycling in soils, and some studies have reported that fungal community biomass, richness and composition varied across soil depths (Fierer et al., 2003). However, it is not clear whether the relationship between fungal community and chemical structure of SOC was different between top- and subsoils (Jumpponen et al., 2010; Weber et al., 2013).

The chemical composition of SOC has been characterized by various methods, among which the solid-state ^{13}C nuclear magnetic resonance spectroscopy (^{13}C NMR) has an advantage of enabling us to obtain information on chemical structure of organic C of the entire soil sample without any physical or chemical fractionation (Huang et al., 2008). A number of studies have linked C forms to microbial community composition, and these studies examined shifts in microbial communities commonly by employing the fungal markers - PLFAs (Cusack et al., 2011; Ng et al., 2014; Wang et al., 2015). Although PLFA compositions have been widely used to characterize the abundance of main microbial groups, the specificity between PLFA markers and certain microbial groups is not high (Ying et al., 2013). DNA-based methods, especially PCR-based methods, greatly improved the sensitivity and specificity in detecting different groups of microorganisms (Ying et al., 2013). However, to our knowledge, there have been few studies on linking the chemical composition of SOC with the structure and function of the fungal community.

The temporal dynamics of the soil fungal community and SOC chemical composition needs to be investigated in order to elucidate their relationships. The chronosequence approach provides information on temporal changes in soil chemical and biological properties (Johnson and Miyanishi, 2008). In subtropical China, farmers have frequently converted paddy fields to Lei bamboo plantations during the past several decades, due to much higher income for Lei bamboo than for rice production (Jiang et al., 2006), which allowed us to establish a chronosequence of Lei bamboo plantations with different stand ages. Therefore, the objective of this study was to investigate the linkage between shifts in fungal community and changes in SOC chemical composition in intensively managed bamboo plantations. Specifically, the following hypotheses were tested: (1) shifts in soil fungal community structure and abundance are linked to changes in the chemical properties of SOC as affected by organic mulching and heavy fertilization; (2) shifts in cellulose-degrading fungal community based on the *cbhl* gene are linked to the increased cellulose residue or *O*-alkyl C content under intensive management; and (3) the response of soil fungal community and C fractions to intensive management is more sensitive in the top- than in the subsoil.

2. Materials and methods

2.1. Experimental site

The study site was located in Taihuyuan township (30°16' N, 119°34' E), within the municipality of Lin'an, Zhejiang Province, China. This area belongs to a typical central subtropical climate with an annual mean temperature of 15.9 °C and a mean annual precipitation of 1628 mm between 2004 and 2013 (Zhang et al., 2013). The study area is 180 m above sea level. The soils in the experimental site were classified as Anthrosols in the FAO soil classification system (WRB, 2006). Sampling plots (see below) were established in 2014. This area was formerly used for paddy rice production for more than 200 years according to the records of the local land-use history. In the last several decades, farmers have

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