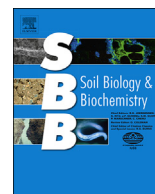




Contents lists available at ScienceDirect

## Soil Biology &amp; Biochemistry

journal homepage: [www.elsevier.com/locate/soilbio](http://www.elsevier.com/locate/soilbio)

## Linkage of microbial residue dynamics with soil organic carbon accumulation during subtropical forest succession



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### ARTICLE INFO

#### Article history:

Received 30 September 2016

Received in revised form

29 June 2017

Accepted 7 July 2017

Available online 19 July 2017

#### Keywords:

Amino sugars

Microbial residues

Soil organic carbon accumulation

Subtropical forest succession

Litter quality

### ABSTRACT

It has been recognized that the formation and subsequent sequestration of soil organic carbon (SOC) during forest succession are primarily driven by soil microorganisms. However, the time-integrated microbial influence on long term SOC accumulation remains unknown. In a subtropical forest succession including three stages of early coniferous forest, middle mixed species forest and climax broad-leaved forest, we investigated changes in soil amino sugars, a biomarker of microbial residues, along a successional gradient to evaluate contributions of fungal and bacterial residues to SOC accumulation over time.

Both the concentrations and stocks of SOC and amino sugars increased with forest succession in the 0–40 cm soil depth, suggesting a close association of microbial proliferation–mortality processes with the sequestration of SOC. In the early successional stage, the contribution of microbial residue-carbon to SOC was low due to the decomposition resistance of needle leaf litter. The later invasion of broad-leaved trees increased the contribution of microbial residues to SOC formation, but the accumulation of amino sugars was more rapid than SOC from early to middle stage, possibly implying that both the production and retention of microbial residues were the essential prerequisite for SOC sequestration. Given the preferences of bacteria to available substrate while the advantage of fungi in using the more recalcitrant part, the proportion of fungal residue-carbon in SOC was significantly larger in the middle stage (mixed forest) while bacterial residues were more prone to accumulate in SOC in the climax stage (broad-leaved forest). The sequestration of SOC along the subtropical forest succession possibly underwent a first stage of accumulation of fungal residues followed by the preferential accumulation of less recalcitrant bacterial residues.

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### 1. Introduction

Forest succession is a fundamental ecological process in terrestrial plant growth (Bruehlheide et al., 2010). During forest succession, both biotic and abiotic characteristics exhibit systematic changes, including plant community structure and productivity

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(Guariguata and Ostertag, 2001; Bruehlheide et al., 2010). Soil microorganisms play an important role in degradation of plant debris, and consequently, the formation of soil organic carbon (SOC). The changing quantity and quality of plant inputs with forest succession are closely associated with altered biomass, activity and community structure of soil microorganisms (Wardle et al., 2004; Banning et al., 2011; Schmidt et al., 2015; Smith et al., 2015). Thus the role of microbial turnover on SOC accumulation during forest succession attracts intensive attention (Gleixner, 2013).

The shift of microbial community structure and the strategy of microorganisms for substrate utilization along forest succession

has been investigated and indicated by viable microbial biomass biomarker such as phospholipid fatty acids (Fierer et al., 2003; Steenwerth et al., 2008; Wei et al., 2015). However, microorganisms are sensitive to both changing substrates and environmental conditions at the sampling point (e.g., temperature and moisture), thus it is difficult to establish the correlation of instantaneous response of living microbial biomass with long term SOC sequestration (Liang and Balsler, 2008). Essentially, microorganisms mediate SOC turnover through the chain of proliferation, metabolism and mortality (Ludwig et al., 2015; Schmidt et al., 2015), thus microbial residues can represent the legacy of considerable microbial derived constituents involved in long term SOC formation (Amelung et al., 2008; Liang et al., 2008). Amino sugars are important microbial residue biomarkers in soil (Stevenson, 1983; Amelung et al., 2001). In the quantified amino sugars, muramic acid (MurN) is uniquely originated from bacterial peptidoglycan. Glucosamine (GluN) is the monomer of fungal chitin and it is also found in bacterial peptidoglycan bonded to MurN at a molar ratio of 2:1. The origins of galactosamine (GalN) remain controversial in spite of its considerable content in soil (Engelking et al., 2007). Indeed, the estimation of soil amino sugars can indicate time-integrated substrate immobilization and microbial community structure (Glaser et al., 2004), which cannot be obtained from those point-to-point microbial biomarkers. This memory effect of amino sugars is useful for indicating the distinct dynamics of bacterial and fungal residues in SOC turnover (Liang et al., 2011). However, one important but little-understood aspect is the dynamics of amino sugars in response to the altered litter inputs along natural forest succession. The lack of such information may retard recognition of microbial function in shaping the chemical composition and long term sequestration of SOC during forest succession.

Subtropical forests provide an important contribution to global terrestrial ecosystem C storage (Zeng et al., 2013; Wang et al., 2015). Because of the monsoon climate with an abundance of heat, light and water resources, the dynamics of SOC in the moist subtropical forests in southern China are highly dependent on the substrate preference of microorganisms and the retention of microbial derived constituents (Tang et al., 2006; Wan et al., 2015). Along the successional gradient from coniferous to broad-leaved forest, different types of litter inputs exhibit a remarkable influence on the response of bacterial and fungal groups (Liu et al., 2012), possibly resulting in distinct microbial residue retention patterns and different microbial functions during SOC accumulation. Therefore, we selected a successional gradient of forest in the Dinghushan, Guangdong Province, and investigated the dynamics of amino sugars in soil profiles. We hypothesized that the contribution of microbial residues to SOC would increase during forest succession because of the improved quantity and quality of substrates, but that the functions of fungal and bacterial residues in terms of carbon (C) sequestration would depend on successional stages due to the distinct substrate utilization strategy of fungal and bacterial groups. This study would provide the first-hand information in interpreting

the long-term microbial functions in terms of SOC sequestration during forest succession in the subtropical region.

## 2. Materials and methods

### 2.1. Site description

The Dinghushan Biosphere Reserve is located at 23°9' to 23°12'N latitude and 112°31' to 112°34'E longitude. This region has a typical subtropical monsoon climate, with an annual average temperature of 21 °C and relative humidity of 80%. The mean annual rainfall is approximately 1956 mm; nearly 80% of the precipitation occurs in the hot-humid season (from April to September) and 20% occurs in the cool-dry season (from October to March). The terrain is quite hilly, with an altitude varying from 10 to 1000 m a.s.l. in most areas. The bedrock of all three forest types is sandstone and shale from the Devonian period. Soils are classified as Oxisols according to the Keys to Soil Taxonomy (Soil Survey Staff, 2003). The general characteristics of the sites are listed in Table 1.

For our study, a natural successional sequence of the forest communities was selected from this biosphere reserve, including early successional *Pinus massoniana* forest (coniferous forest, about 50–60 years), middle successional coniferous and broad-leaved species mixed forest (mixed forest, about 100–110 years) and climax successional monsoon evergreen broad-leaved forest (broad-leaved forest, more than 400 years). The coniferous forest was dominated by *Pinus massoniana* in the canopy tree layer. Dominant tree species were *Pinus massoniana*, *Shorea superba* and *Cercis chinensis* in mixed forest and *Cercis chinensis*, *Castanopsis concinna*, *Erythrophleum fordii*, and *Cyathea podophylla* in broad-leaved forest (Peng and Wang, 1995). Detailed information on the successional fields were described in Tang et al. (2006) and Zhou et al. (2007).

### 2.2. Soil and litter sample collection and preparation

In February 2012, three plots (50 m × 50 m square) were selected in each of the three successional forests, with a minimum distance of 10 m between any two plots. To minimize the topographic disturbance on soil sampling, all selected plots were located in gentle slope areas. In each sampling plot, three individual samples of organic and mineral layers were randomly collected and mixed to form a composite sample.

Before collecting soil samples, we identified and collected the organic layer (un-decomposed layer). After removing the organic layer, soil samples were collected at 0–10 cm, 10–20 cm and 20–40 cm layers, respectively.

Organic samples were oven-dried at 65 °C for 12 h, and soil samples were air-dried for 3–7 days. Plant roots were then removed with a 2 mm sieve. Organic and mineral samples were ground in an agate mortar and sieved to less than 0.149 mm for organic carbon (OC) and total nitrogen (TN) measurements (elemental analyzer, Model CN, Vario Macro Elemental Analyzer

**Table 1**  
General characteristics of the study sites.

Successional stage	Forest type	Latitude and longitude	Bulk density <sup>a</sup> (g cm <sup>-3</sup> )		Mean annual litterfall production <sup>b</sup> (g m <sup>-2</sup> )	Soil microbial biomass at 0–10 cm layer <sup>c</sup> (mg kg <sup>-1</sup> )
			0–10 cm	10–20 cm		
Early	Coniferous forest	23.11 N, 112.34 E	1.34 ± 0.04	1.47 ± 0.04	356	193–449
Middle	Mixed forest	23.11 N, 112.33 E	1.24 ± 0.03	1.36 ± 0.04	861	368–569
Climax	Broad-leaved forest	23.11 N, 112.33 E	1.06 ± 0.02	1.37 ± 0.03	849	522–1022

<sup>a</sup> Data of bulk density were cited from Mo et al. (2003).

<sup>b</sup> Data of mean annual litterfall production were cited from Zhou et al. (2007).

<sup>c</sup> Data of soil microbial biomass were cited from Huang et al. (2013) and Zeng et al. (2013).

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