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Microbial Residue Distribution in Microaggregates Decreases with Stand Age in Subtropical Plantations

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Abstract: Soil microbial residues contribute to the majority of stable soil organic carbon (SOC) pools, and their distribution among aggregate fractions determines long-term soil carbon (C) stability and, consequently, soil productivity. However, how microbial residue accumulation and distribution respond to stand age remains unexplored. To fill this knowledge gap, we investigated microbial residues in bulk soil and soil aggregate fractions under a chronosequence of Chinese fir (*Cunninghamia lanceolata* [Lamb.] Hook) plantations with stands aged 3, 17, 27, and 36 years. The results showed that microbial residues in topsoil did not change across the different stand ages, but the residues in the subsoil increased from 3 to 17 years of age and then remained constant. Moreover, microbial residue distribution in microaggregates decreased with stand age, and the residue distribution in small macroaggregates was lower at age 17 years than at other stand ages. The effect of stand age on microbial residue distribution was due to the fact of their effect on aggregate distribution but not microbial residue concentrations in aggregate fractions. Collectively, our results indicate that microbial residue stability decreased with stand age, which has significant implications for the management of SOC in subtropical plantations.

Keywords: stand age; amino sugars; soil aggregates; subtropical plantation

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1. Introduction

Soil organic carbon (SOC) is the largest terrestrial carbon (C) reservoir, and its maintenance determines long-term soil productivity [1]. Microbial residues contribute to ~60% of SOC in the mineral soil of global forests [2,3]; their long residence times are due to the physical protection of aggregate occlusion, and mineral adsorption makes them a significant source of stable SOC pool, playing a vital role in long-term SOC sequestration [4]. Residues have been widely estimated using biomarker amino sugars, which are the key components of microbial cell walls [2,4]. Even so, current studies are mainly conducted on bulk soil without considering microbial residue distribution among aggregates. Given that soil aggregate fractions differ greatly in their physical protection capability [5], understanding microbial residue distribution in soils can provide more information on SOC stabilization and, in turn, soil productivity management.

Forest plantations have widely been considered as an effective way to increase SOC sequestration [6,7]. As a result, China has continuously established forest plantations for decades, and now plantation areas in China occupy first place in the world [8,9]. Chinese

fir (*Cunninghamia lanceolata* [Lamb.] Hook) is one of the most planted species in forest plantations; its area accounts for 18.2% of all plantations in China [9]. With increasing timber demand, clear-cut and afforestation of Chinese fir plantations alternatively occurs, resulting in different stand ages co-existing [10,11]. Previous studies have shown that stand age in these plantations significantly influenced SOC [12,13] and soil aggregate distribution [14]. However, how stand age affects microbial residues, and their distribution in soil aggregates remains unexplored. Moreover, Ni et al. [2] reported that microbial residues changed with soil depth in global forest soils. Therefore, microbial residues and their distribution among aggregates in response to stand age may differ at different soil depths. However, direct evidence for this assumption is lacking. Filling these knowledge gaps is urgently needed to predict SOC dynamics and their potential feedback to forest management in plantation ecosystems.

Here, we investigated microbial residues at two depths of mineral soil in Chinese fir plantations differing in stand age (including aged 3, 17, 27, and 36 years). The main objectives of this study were to (1) investigate how stand age, alone and its interaction with soil depth, affect soil microbial residues and their distribution among aggregates; (2) examine how environmental factors and soil microbial communities affect microbial residue accumulation.

2. Materials and Methods

Our study site was located at the Huitong Experimental Station of Forest Ecology (26°40′ N, 109°26′ E), Hunan Province in southern China. The climate is subtropical monsoon humid, with a mean annual rainfall of 1200–1400 mm and a mean annual temperature of 16.5 °C [15]. The soil is classified as typical lateritic developed from slate and shale parent rock [11]. This study site used to be an evergreen broad-leaved forest dominated by Cyclobalanopsis, Castanopsis, Lithocarpus, and Machilus, with the dominant shrubs of *Loropetalum chinensis* (R.Br.) Oliv., *Eurya chinensis* Brown, 1818, *Camellia oleosa* C. Abel, and *Rhus semialata* Mill.. Since the 1960s, forests in this region have been widely replaced with fast-growth commercial Chinese fir (*Cunninghamia lanceolata* [Lamb.] Hook). After harvest in the 1980s, intermittent reforestation of Chinese fir was carried out between 1985 and 2014 [11]. Therefore, the field station has a chronosequence of existing Chinese fir plantations, covering from young to mature stands. The growth rate of these stands increased from young to premature stands and then decreased [11].

In this study, a chronosequence of four differently aged Chinese fir stands (i.e., 3, 17, 27, and 36 year old stands, which correspond to young, middle-aged, premature, and mature stands according to Xia et al. [16]) was carefully selected from eight 2 ha permanent plots with the same land-use history and management practices in June 2018. Four plots (15 × 15 m) were established in each plantation per age category. At each plot, seven random soil cores (0–10 cm) were taken, homogenized to one composite sample, sieved through an 8 mm sieve, and divided into two subsamples: one that was further passed through a 2 mm sieve for soil chemical properties, microbial communities, and microbial residues analysis; the other was used to separate soil aggregate fractions.

Air-dried soil samples were analyzed for SOC and total nitrogen (TN) on a C/N analyzer (Elementar, Darmstadt, Germany). Total phosphorus (TP), available phosphorus (AP), available potassium (AK), and soil exchangeable cations (ECs; including K^+, Na^+, Ca^{2+}, and Mg^{2+}) were quantified using the typical methods described in [17]. Soil pH was determined with a pH meter using a water-to-soil ratio of 2.5:1. The field-moist sieving method was used to separate soil aggregate fractions [15]. Briefly, 100 g fresh soils with soil moisture below 15% were put on a nest of two sieves (2 and 0.25 mm), mounted on a sieving machine (Retsch AS200 Control, Retsch Technology, Dusseldorf, Germany), and shook for 2 min with a 1.5 mm amplitude. Then, the soils on the 2 mm sieve (i.e., large macro-aggregates; LMAs), on the 0.25 mm sieve (i.e., small macro-aggregates; SMAs), and under the 0.25 mm sieve (i.e., micro-aggregates; MAs) were weighed and air-dried for future use.

Phospholipid fatty acids (PLFAs) analysis were conducted to assess the bacterial biomass and fungal biomass [18]. In brief, PLFAs were extracted from 5 g of freeze-dried soil with a chloroform:methanol:phosphate buffer. After being purified and separated, the PLFAs were identified using an Agilent 6850 gas chromatograph (Agilent Technologies, Santa Clara, CA, USA). The PLFA markers representing fungi were 18:2 w6c and 18:1 w9c; representing bacteria were a11:0, a12:0, a13:0, i13:0, i14:0, a14:0, i15:0, a15:0, i16:0, a16:0, i17:0, a17:0, i18:0, 15:1w7c, 15:1w5c, 16:1w7c, 17:1w8c, 17:0 cy, 19:0 cy, 21:1w5c, 16:0 10-methyl, 17:0 10-methyl, 18:0 10-methyl, 12:0, 14:0, 15:0, 16:0, 17:0, 18:0, 20:0, 22:0, and 24:0 [19].

Microbial residues were estimated based on the biomarker amino sugars, which were extracted, purified, and separated according to Zhang and Amelung [20]. Amino sugar derivatives were identified with an Agilent 7820A gas chromatograph (Agilent Technologies, Santa Clara, CA, USA) equipped with an HP-5 column and flame ionization detector. Bacterial residues were calculated as muramic acid (MurN), multiplying at an average conversion factor of 45; fungal residues were calculated as (mmol glucosamine $-2 \times$ mmol MurN) $\times$ 179.2 $\times$ 9, where 179.2 is the molecular weight of glucosamine, and nine is the average conversion factor from glucosamine to fungal residues [21]. Microbial residues were calculated as the sum of bacterial and fungal residues. The microbial residue distribution in *i*th size fractions was calculated as Pi $\times$ CCi $\div$ CC [22], where Pi is the proportion of the *i*th size aggregates, CCi is the microbial residue content in the *i*th size aggregate, and CC indicates the microbial residue content in bulk soil.

The Shapiro–Wilk normality test was performed for all variables to determine the normal distribution, and Levene's tests was conducted to check the homogeneity of variance. Linear mixed-effects models were used to analyze the effect of stand age (A), soil depth (D), and their interaction on soil properties, microbial biomass, microbial residues, and their distribution among different aggregate fractions, with A and D as fixed effects and the site as a random effect. A Duncan's test was conducted to assess the differences among stand age at $p < 0.05$. Structural equation modeling (SEM) was created to determine the control of variables on microbial residues in bulk soil (R 3.4.1 with the "lavaan" package). An insignificant chi-square test (χ^2, $p > 0.05$), a comparative fit index (CFI) over 0.9, and χ^2/df within 0–2 represent that the SEM was acceptable [22]. All statistical analyses were conducted using R version 3.4.1.

3. Results

Stand age did not affect SOC, AK, pH, EC, soil aggregate distribution, bacteria, and fungi but significantly affected the C/N ratio (A: $p < 0.01$; D $\times$ A: $p < 0.01$) and C/P ratio (A: $p < 0.01$; D $\times$ A: $p < 0.01$). Specifically, a higher C/N ratio was observed in the subsoil for the 17 year old stand, but a higher C/P ratio was observed in the topsoil of the 3 year old stand (Table 1). Across all stands, the topsoil was more nutrient-rich than the subsoil. The SOC, C/N ratio, C/P ratio, AK, pH, and EC were 83.8%, 41.9%, 123.1%, 59.0%, 13.1%, and 29.3% higher in topsoil than in subsoil, respectively (all $p < 0.001$; Table 1). However, the proportion of large macroaggregates (LMAs) was 9.1% lower; however, the microaggregates (MAs) were 29.1% higher in topsoil than in subsoil ($p = 0.016$ and $p < 0.001$, respectively; Table 1).

Stand age interacted with soil depth to affect microbial residue accumulation (D $\times$ A: $p = 0.03$; Figure 1), while it had no impact on microbial residues in SOC (Figure S1). Specifically, microbial residues in the subsoil increased from 3.3 g·kg^{-1} at age 3 years to more than 5 g·kg^{-1} at age > 17 years ($p < 0.05$; Figure 1). Moreover, microbial residues were 86.2% higher in the topsoil than in the subsoil ($p < 0.001$; Figure 1). The SEM showed that soil nutrients (i.e., available potassium and the C/N ratio) had direct positive effects on microbial residue accumulation (Figure 2).

Table 1. Soil properties of different tree species plantations at two depth intervals.

Stand Age (year)	Depth (cm)	SOC (g kg^{-1})	C/N	C/P	AK (mg kg^{-1})	pH	EC (mg kg^{-1})	Soil Aggregate Distribution (%)			Bacteria (mg kg^{-1})	Fungi (mg kg^{-1})
								LMA	SMA	MA		
3	Topsoil	20.4 ± 0.6	11.9 ± 0.4	73.5 ± 1.5a	56.3 ± 2.0	4.84 ± 0.01	311.0 ± 2.5	48.2 ± 0.5	41.7 ± 0.6	10.1 ± 0.9	6.5 ± 0.9	0.4 ± 0.0
17		20.1 ± 1.4	12.1 ± 0.5	36.5 ± 1.7b	38.1 ± 7.0	5.16 ± 0.11	255.5 ± 15.2	44.9 ± 0.2	42.5 ± 2.3	12.6 ± 0.4	7.8 ± 0.5	0.4 ± 0.0
27		19.5 ± 1.9	11.7 ± 1.1	34.5 ± 4.4b	52.1 ± 5.2	4.86 ± 0.05	349.0 ± 3.5	48.3 ± 3.1	43.0 ± 0.5	8.7 ± 0.8	7.6 ± 0.9	0.6 ± 0.1
36		20.9 ± 1.1	11.7 ± 0.5	40.1 ± 5.0b	49.2 ± 6.6	4.65 ± 0.04	320.0 ± 29.2	52.2 ± 0.7	39.6 ± 0.6	8.2 ± 0.4	7.2 ± 0.8	0.5 ± 0.1
3	Subsoil	8.5 ± 1.3	8.0 ± 1.0b	16.7 ± 3.8	29.8 ± 2.5	4.30 ± 0.00	246.3 ± 21.1	51.3 ± 1.6	40.0 ± 1.7	8.7 ± 0.4	4.5 ± 0.7	0.4 ± 0.1
17		14.4 ± 2.2	10.6 ± 0.4a	25.7 ± 8.8	28.0 ± 3.03	4.26 ± 0.05	221.0 ± 7.47	64.1 ± 3.3	28.3 ± 3.5	7.7 ± 0.4	6.4 ± 0.8	0.4 ± 0.1
27		11.5 ± 1.6	6.7 ± 0.7b	17.4 ± 3.8	38.7 ± 4.4	4.26 ± 0.03	270.5 ± 8.6	51.2 ± 1.2	41.7 ± 1.2	7.2 ± 0.2	6.1 ± 1.1	0.0 ± 0.1
36		10.7 ± 0.8	8.5 ± 0.4b	18.3 ± 1.4	28.8 ± 1.3	4.3 ± 0.04	249.9 ± 10.9	49.2 ± 1.2	43.3 ± 0.5	7.5 ± 0.8	7.6 ± 0.8	0.0 ± 0.0

Data are shown as the mean ± SE. SOC, soil organic carbon; C/N, SOC/TN ratio; C/P, SOC/TP ratio; AK, available potassium; ECs, exchangeable cations; LMAs, large macroaggregates; SMAs, small macroaggregates; MAs, microaggregates.

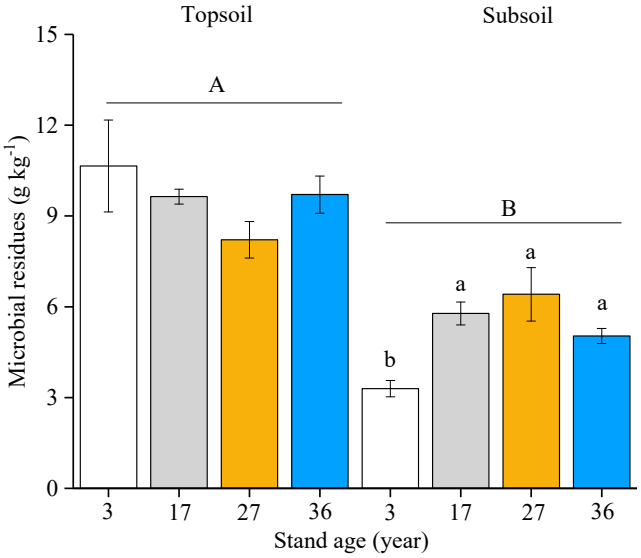

Figure 1. Microbial residues in bulk soil across the Chinese fir chronosequence in southern China. Different uppercase letters indicate significant differences ($p < 0.05$) between soil depths. Different lowercase letters indicate significant differences ($p < 0.05$) among stand ages at the same soil depth. Values are the mean ± SE.

Stand age interacted with soil depth to affect microbial residue distribution in SMA (D × A: $p = 0.032$), with a lower value at 17 years of age in the subsoil. Microbial residue distribution in MAs decreased with stand age ($p < 0.001$; Figure 3), which was 31.7% lower at 36 years of age than at 3 years of age, regardless of soil depth. Soil depth did not affect microbial residue distribution in LMAs or small macroaggregates (SMAs), but a higher microbial residue distribution in MAs was observed in topsoil than in subsoil ($p < 0.001$; Figure 3).

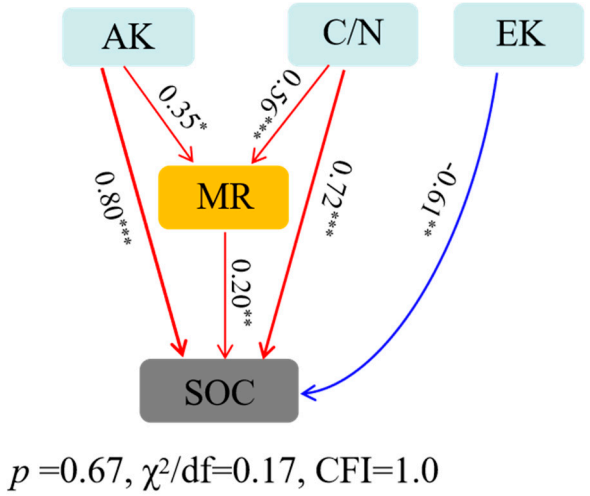

Figure 2. Structural equation modeling (SEM) for the control of microbial residues and soil organic matter (SOC) in the top 20 cm of soil at Chinese fir plantations. The red and blue arrows represent positive and negative relationships, respectively. The numbers next to arrows are standardized direct effects. *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$. AK, soil available potassium; EK, soil exchangeable potassium; C/N, SOC/TN ratio; MRs, microbial residues; CFI, comparative fit index.

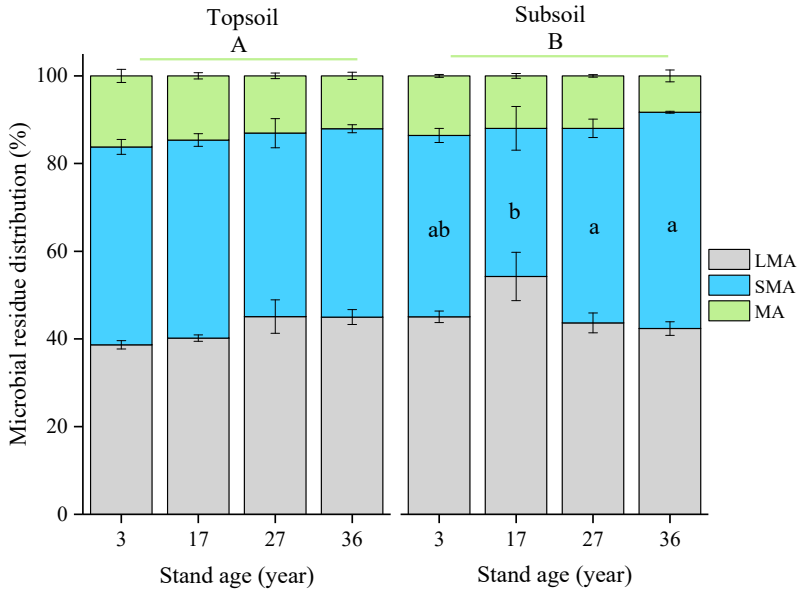

Figure 3. The distribution of microbial residues among aggregates in topsoil and subsoil across the Chinese fir chronosequence in southern China. Different uppercase letters indicate significant differences ($p < 0.05$) between soil depths. Different lowercase letters indicate significant differences ($p < 0.05$) among stand ages at the same soil depth. LMAs, large macroaggregates; SMAs, small macroaggregates; MAs, microaggregates. Values are the mean ± SE.

4. Discussion

To date, no studies have been conducted on the relationships between stand age and microbial residue accumulation and distribution among aggregates. The current study presents the first attempt to investigate how stand age affects microbial residue accumulation and distribution in topsoil and subsoil in subtropical Chinese fir plantations. We found that stand age did not affect microbial residues in topsoil, but higher microbial residues were observed in subsoil at age ≥ 17 years of age than at three years of age (Figure 1). This result indicates that microbial residues in the subsoil were sensitive to stand age, but not generally believed to be so for topsoil. Although we found that soil available potassium

and the C/N ratio both had positive effects on microbial residues (Figure 2), changes in these variables could not explain our results, because they did not show similar response patterns to stand age (Table 1). Roots promote the formation of microbial residues [23,24], because microbial growth highly depends on root-derived labile C [25]. Compared with the middle-aged, premature, and mature stands, the young stand had a much lower root biomass in the subsoil (i.e., 10–20 cm) [26]. Moreover, the young stand of Chinese fir had the lowest growth rate among the four stands [11], meaning they have lowest litter C inputs, which provide new energy for microbes [27], especially in subsoil. Taken together, this may explain the response pattern of microbial residues in the subsoil to stand age. The constant microbial residues in topsoil reflected the balance between their formation and decomposition with stand age. These two processes are both closely dependent on substrate conditions [28,29], which changes with stand age via aboveground litter inputs, root growth, and nutrient uptake in Chinese fir plantations [12,16,30].

Moreover, we found that more microbial residues accumulated in topsoil than in subsoil (Figure 1). This result is consistent with those obtained using a recent meta-analysis database of forest soils (Figure S2). In the current study, higher available potassium and C/N ratio were responsible for more microbial residues in topsoil according to the SEM result (Figure 2). Potassium is the third most essential macronutrient for plant growth [31]. An appropriate amount of potassium benefits photosynthate production and facilitates root growth [32]. Potassium is a limited nutrient in the study site due to the fact of weathering and poorly developed soil structure [33] as well as the lack of potassium fertilization. Therefore, higher available potassium in topsoil than in subsoil ($p < 0.001$; Table 1) likely leads to more plant C input and, consequently, contributes to more microbial residues via microbial metabolisms. The important role of potassium in microbial residues was also found in another study we conducted (unpublished result) but not anywhere else. Therefore, more studies across different sites are needed to test whether the potassium role in microbial residues is general. Higher microbial residues accompanied by higher soil C/N ratio is consistent with previous studies [24,34]. Microbial residues are formed by heterotrophic microbes which need C as their energy to grow [25]. Thus, a higher C/N ratio in topsoil could lead to more microbial biomass production and increase their residue accumulation with biomass turnover.

In addition to the microbial residue content, we found that the microbial residue distribution was also sensitive to stand age. Lower microbial residue distribution in SMAs at age 17 years than at age 27 and 36 years in subsoil (Figure 3) was due to the lower proportion of LMAs (Table 1), given that the microbial residue content in LMAs at 17 years old was higher than other stand age (data not shown). Moreover, we found that microbial residue distribution in MAs decreased with stand age (Figure 3). Considering that microaggregates have a stronger physical protection capacity than macroaggregates [5], this finding indicates that the microbial residue stability decreases with an increase in the age Chinese fir. This result was due to the fact of a stand age-induced decrease in the proportion of MAs. However, this was not the case for the effect of soil depth on microbial residue distribution in MAs. Higher values in the topsoil than in subsoil was the combined result of higher microbial residue content in MAs and a higher proportion of MAs (Table 1). Topsoil has many more roots than subsoil [26], which can generate more microaggregates (e.g., 2–20 μm size) at the soil–root interface [35]. Moreover, more roots generally increase mycorrhiza fungi infection, and these fungi and their mycelium not only form a number of fungal residues [36] but also enmeshes particles into microaggregates [5]. Thus, microbial residue distribution in topsoil was determined by both aggregate-associated content and aggregate proportion. Token together, physical protection of microbial residues should be considered to accurately predict soil C dynamics at long-term scales in plantation ecosystems.

5. Conclusions

The results of this study demonstrated that the microbial residues in subsoil increased from 3 years of age to 17 years of age and remained constant, while the stability of the

microbial residues decreased with stand age, indicated by the reduction in microbial residues in microaggregates. Moreover, the available potassium and C/N ratio positively affected microbial residue accumulation. Further research is needed to test whether the potassium role in microbial residues is general. This work offers new insights into the age-specific effect on microbial functioning and provides important information on soil C prediction and management in plantation ecosystems.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/f13071145/s1, Figure S1: Microbial residues in SOC across the Chinese fir chronosequence in southern China; Figure S2: Microbial residues in topsoil and subsoil at a global scale. Reference [2] is cited in the supplementary materials.

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