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RESEARCH ARTICLE

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Accumulation of glomalin-related soil protein benefits soil carbon sequestration: Tropical coastal forest restoration experiences

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Abstract

Many tropical coastal areas experience severe soil erosion due to heavy rainfall, especially after deforestation. Glomalin-related soil protein (GRSP), the product of arbuscular mycorrhizal fungi (AMF), improves soil structure and soil organic carbon (SOC) sequestration with vegetation restoration. Therefore, the contribution of GRSP to soil property improvement in a tropical coastal area was studied for four different restoration practices: a barren land (BL, unrestored control), a *Eucalyptus exserta* planted forest (EF), a mixed broadleaved forest (MF), and a secondary natural forest (SF). Results showed that vegetation restoration practices increased easily-extractable GRSP (EE-GRSP) and total GRSP (T-GRSP) by 3.9–12.3- and 1.9–4.6-times, respectively, compared with BL. The proportions of EE-GRSP/SOC and T-GRSP/SOC were 1.6%–2.0% and 6.5%–15.8%. The concentrations of GRSP, SOC, and the GRSP/SOC ratio were similar or greater under MF than under SF. ^{13}C NMR analysis showed that the relatively easily degradable O-alkyl-C of SOC was significantly higher under MF than under EF and SF, while the recalcitrant aromatic-C or alkyl-C were highest under SF or EF, respectively. A significantly positive relationship was found between the GRSP/SOC ratio and aromatic-C, and between GRSP and soil aggregate stability. Our study indicates that GRSP contributes to a large proportion of SOC, and benefits SOC sequestration through increasing soil aggregate stability and recalcitrant SOC. Among these artificial or naturally growing forest areas, a mixed forest restoration practice with native tree species provides a promising restoration strategy for heavily eroded land restoration, in particular improving soil aggregation and SOC sequestration.

KEYWORDS
Eucalyptus exserta forest, mixed broadleaved forest, secondary natural forest, soil aggregate, soil carbon chemical composition

Jing Zhang and Jian Li contributed equally to this study.

1 | INTRODUCTION

Forests cover one-third of the World's total land area and store over one-half of the global soil organic carbon (SOC), playing a crucial role in the global carbon (C) cycle (Kuuluvainen & Gauthier, 2018; Zhu et al., 2017). Forest ecosystems can be successfully managed to increase C sequestration by restoring vegetation, but if improperly managed it can decrease SOC stock through vegetation degradation (Tang et al., 2018). Most C, mainly in the form of SOC, is stored in soil rather than plants. Therefore, even a small change of the SOC pool in forest ecosystems could have far-reaching effects on the global C cycle. Reforestation and afforestation are common practices that can contribute to offsetting CO_2 emissions because the growth of plants sequesters atmospheric CO_2 and stores it in plants and soil. As a result, large afforestation and reforestation programmes have been undertaken worldwide with an area estimated at 26.7 million ha converted between 2000 and 2019 (FAO, 2020). The afforested/reforested forest area in China increased was annually by 2 million ha between 1990 and 2000, and by 3 million ha from 2000 to the present. Worldwide afforestation has resulted in an estimated total emission reduction of 4.4 million t CO_2 equivalent (FAO, 2020; Zhou et al., 2017).

Studies have shown that arbuscular mycorrhizal fungi (AMF) play an important role in forest restoration in eroded areas with infertile soils at the early-middle restoration stage (Asmelash et al., 2016; Wang et al., 2019). AMF colonize approximately 80% of terrestrial vascular plants (Smith & Read, 2008) and contribute to plant vigour by improving nutrient uptake and enhancing their survival in adverse soil (Asmelash et al., 2016; Bonfim et al., 2013). AMF improves the stability of soil aggregates because of their rich hyphae (Morris et al., 2019). AMF have also been proven to contribute to soil C accumulation because aboveground plants allocate approximately 4%–20% of photosynthates to belowground symbiotic AMF (Bago et al., 2000). Also, AMF deposit slow-cycling organic products, such as chitin and glomalin, into the soil (Smith & Read, 2008). The latter is an important SOC component (Treseder et al., 2007) that contributes to the mitigation of multiple soil degradation problems (Singh et al., 2020).

Glomalin, a hydrophobic glycoprotein, is more properly referred to as glomalin-related soil protein (GRSP) (Rillig, 2004). In general, GRSP contains 3%–5% of N and ~20%–59% C which accounts for up to 40% of SOC (He et al., 2010; Lovelock et al., 2004; Schindler et al., 2007). GRSP accumulates with soil chronosequence (Kumar et al., 2018; Rillig et al., 2001) and enriches soil with recalcitrant aromatic-C that can reside underground for decades (Schindler et al., 2007; Wang et al., 2020). Hence, GRSP could benefit ecological restoration by affecting soil biotic and abiotic factors including soil physical properties, microbial activities, and soil nutrients, etc. (Liu et al., 2020; Qiao et al., 2019; Singh et al., 2020). However, studies are limited for grasslands (Liu et al., 2019), farmlands (Welemariam et al., 2018), monocultures (Santos & Scotti, 2018), and temperate forests (Qiao et al., 2019), and little is known about tropical coastal forests where soil erosion is heavy.

The restoration of trees is urgent because the canopy cover may decline by 223 million ha globally by 2050, with the vast majority of this loss in the tropical areas (Bastin et al., 2019). In the early-1950s, tens of thousands of hectares of soil had been degraded in the tropical coastal area in southern China due to severe erosion after massive deforestation (Ren et al., 2007). Studies have found that GRSP increased with vegetation recovery time in forests (Qiao et al., 2019) and grasslands (Liu et al., 2019) in the Loess Plateau of northwest China. However, whether GRSP has also accumulated, given the timing of forest restoration in the tropical coastal erosion area of southern China is not clear. Several restoration activities have been conducted to improve the severely eroded lands since the 1950s in southern China. The purpose of our study was to reveal the accumulation pattern of GRSP and its contribution to SOC sequestration under the four study forest restoration practices. A series of restoration programmes have been undertaken in the tropical coastal area of southern China. These restoration activites started in 1959 and can be grouped into the following ctegories: (1) barren land (BL); (2) *Eucalyptus exserta* plantation forest (EF); (3) mixed broadleaved forest (MF); and (4) secondary natural forest (SF), representing the unrestored control. There have been two different restoration practices and a future scenario can be recognized. Previous studies of these restored forests have shown that vegetation biomass production and SOC stock had markedly increased (Wu et al., 2021; Zhang et al., 2019) with the restoration processes. As to the production of AMF, its contribution to SOC and information on GRSP are not clear; it can be assumed accumulation of the latter varied with the restoration practices. GRSP variations could affect SOC accumulation (GRSP/SOC ratio), and consequently the relationships between GRSP and the recalcitrant SOC or the stability of soil aggregates in these restored forests. The objectives of our study were therefore to test the following hypotheses: (1) GRSP would be varied with forest restoration practices; (2) the proportion of GRSP in SOC would also vary with forest restoration practices; and (3) GRSP would be beneficial to soil C accumulation or sequestration by improving soil aggregates and/or the proportion of recalcitrant SOC. Answers to these questions will enhance our understanding of the roles of GRSP and SOC in forest restoration and could improve strategies.

2 | MATERIALS AND METHODS

2.1 | Study sites and soil sampling

This study explored a series of restoration practice scenarios (Figure 1) in tropical coastal forest ecosystems near the Xiaoliang Station (2 L°27′49″N, 110°54′18″E, 10 m above sea level) in southwest Guangdong, China. The area has a typical tropical monsoon climate with a contrasting dry season (October–April) and wet season (May–September). The annual mean temperature is 23°C and the annual precipitation is about 2000 mm. The climax vegetation in this area has been a monsoon evergreen broadleaved forest with a declined due to logging in the 1950s (Figure 1). The zonal soil is a kind of latosol,

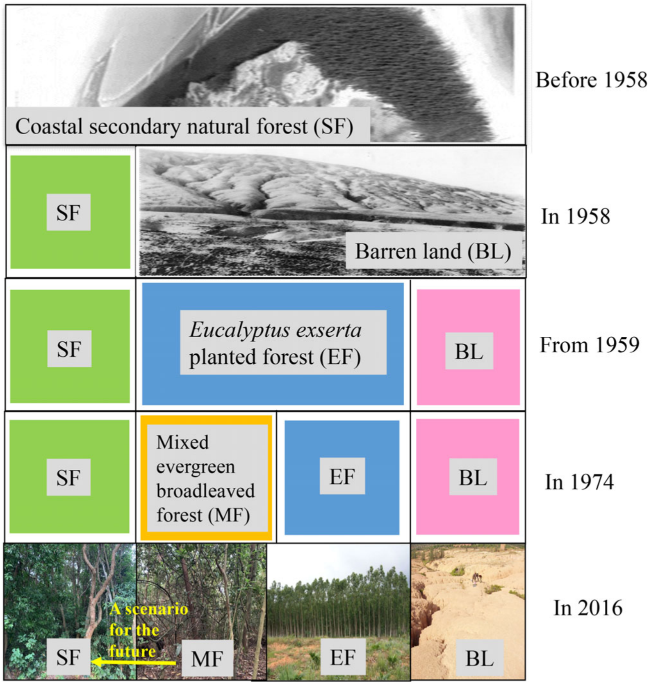

FIGURE 1 Status of forest restoration practices at different times near the Xiaoliang Station in the southwest of Guangdong Province, China. The squares with different colours represent different forests becauseince photos before 2016 were not available. *Note*: The photos or squares sizes of these naturally or artificial forests do not represent the actual areas [Colour figure can be viewed at wileyonlinelibrary.com]

which has developed from granite and has endured heavy erosion since the 1950s in a harsh hydrothermal habitat (Ren et al., 2007; Wu et al., 2021). For instance, with a monthly mean <20% soil moisture, the maximum monthly mean 0–20 cm surface temperature in the bare soil in July is 47.5°C, which is 17°C higher than the ambient air temperature. Soil total C and nitrogen concentrations at 0–20 cm depth are only 0.6% and 0.03%, respectively (Ren et al., 2007).

A series of afforestation practices have been conducted since 1959 on the barren land (BL), although the harsh habitat makes natural vegetation restoration difficult. We selected 3.7 ha of BL that had undergone no human interference since 1959 and were assigned this as the vegetation restoration control. Only a few herbaceous plants or xeric shrubs, including *Dicranopteris pedata* and *Eriachne pallescens*, are to be found, mainly scattered and growing in ditches, because the topsoil has been completely eroded (Ren et al., 2007).

One initial restoration programme was undertaken in the BL with *E. exserta* plantations (7.7 ha) the timber harvested every 5–8 years beginning in the early-1960s (Figure 1). Half of the *E. exserta* plantation area (3.8 ha) was clear-cut in 1974 and a total of 312 species were replanted from 1974 to 2016 by yearly species replacement to build a mixed forest (MF), with an average of 14.6 tree species remaining in 20 × 20 m sample plots in 2016 (Wu et al., 2021). Most plants (replanting with native spcies) in this MF were not directly planted because of the extremely eroded barren soil, a successful growth of pioneer *Eucalyptus* was required, so it took decades (Ren et al., 2007; Wang et al., 2017; Wu et al., 2021). This MF can then develop into a secondary natural evergreen broadleaved forest that is similar to the undisturbed secondary natural forest (SF) (Ren et al., 2007). Our study includes sites that experienced one of four restoration practices or treatments: (1) barren land (BL) as the unrestored control; (2) *E. exserta* plantation forest (EF); (3) planted mixed broadleaved forest (MF); and (4) typical secondary natural forest (SF) (Figure 1). See Ren et al. (2007) and Table 1 for detailed information about soil and microbial properties in this study site.

Based on the simple random sampling method (Kershaw Jr. et al., 2017), we set up five plots (20 × 20 m) as replicated sampling plots for each restoration treatment. The five replication sampling plots were randomly located apart >50 m distance from each other. Seven soil cores (2.5 cm diameter at 10 cm depth) from each replicate plot were randomly collected and mixed as one composite sample (~1.0 kg) for further analysis in June 2016 after the surface litter and humus were removed. A total of 20 (four restoration practices × five replicates) samples were thus collected for the measurement of soil aggregates, GRSP, and soil C chemical composition, etc. Each sample was then divided into two parts or subsamples, one was for aggregates analysis, and the other was passed through a 2-mm mesh sieve for AMF, GRSP, and SOC analysis.

2.2 | Determination of glomalin-related soil proteins

Both the easily extracted GRSP (EE-GRSP) and total GRSP (T-GRSP) were measured by a modified method mentioned by Zhang et al. (2014) based on the Bradford protein assay (Wright & Upadhyaya, 1998). Briefly, EE-GRSP or T-GRSP was extracted by 8 mL of 20 mmol L^{-1} sodium citrate (pH = 7.0) or 50 mmol L^{-1} of sodium citrate (pH = 8.0) from 1.00 g air-dried soil. Then the extractions were autoclaved for 30 (EE-GRSP) or 60 (T-GRSP) minutes at 121°C and centrifuged at 10,000 × *g* for 10 min. The T-GRSP extraction process was performed four times for each sample and then all of the supernatants were pooled together and stored at 4°C before the Bradford analysis. The optical density (OD) value of the GRSP was measured at 595 nm using bovine serum albumin (BSA) as the standard with an enzyme microplate reader (Thermo Multiskan FC, USA).

2.3 | Determinations of soil organic carbon concentration and soil physicochemical properties

Concentrations of SOC and other soil physicochemical properties were measured using the methods described by Liu et al. (1996). Briefly, the SOC concentration was tested by titration with $FeSO_4$ (0.2 mol L^{-1}) after dichromate oxidation (Liu et al., 1996), soil total nitrogen (total N) was measured by the micro-Kjedahl method, and soil total phosphorus (total P) was determined using a microplate reader after samples were digested with nitric acid. The concentration

TABLE 1 Soil nutrient and microbial indexes among the four study forest restoration practices

	BL	EF	MF	SF
Total N (mg g^{-1})	0.35 ± 0.03 d†	1.03 ± 0.06 c	2.15 ± 0.09 b	3.02 ± 0.08 a
Total P (mg g^{-1})	0.09 ± 0.01 c	0.10 ± 0.01 c	0.18 ± 0.01 b	0.43 ± 0.01 a
NO_3^--N (mg kg^{-1})	2.64 ± 0.33 c	1.22 ± 0.24 c	14.86 ± 1.24 b	36.99 ± 2.58 a
NH_4^+-N (mg kg^{-1})	3.30 ± 0.09 b	11.21 ± 0.71 b	38.20 ± 3.43 a	31.14 ± 4.37 a
Available P (mg kg^{-1})	0.50 ± 0.20 c	2.39 ± 0.31 b	5.98 ± 0.35 a	6.98 ± 0.70 a
AMF diversity	–‡	1.56 ± 0.13 b	1.83 ± 0.11 b	2.37 ± 0.05 a
AMF biomass (nmol g^{-1})	0.04 ± 0.02 c	0.18 ± 0.02 c	0.57 ± 0.15 b	1.08 ± 0.08 a
Microbial biomass (nmol g^{-1})	7.40 ± 0.99 b	10.52 ± 0.67 b	32.83 ± 4.90 a	38.14 ± 3.43 a

Abbreviations: AMF, arbuscular mycorrhizal fungi; BL, barren land; EF, *Eucalyptus* forest; MF, mixed broadleaved forest; NH_4^+-N, ammonium nitrogenl; NO_3^--N, nitrate nitrogen; SF, secondary natural forest; Total N, soil total nitrogen; total P, soil total phosphorus

†Different lower-case letters in the same row represent significant differences among the four study forest restoration practices ($p < 0.05$)

‡Data did not obtain due to the AMF being scarce in the BL

of nitrate-nitrogen (NO_3^--N) was tested after cadmium reduction to nitrate, followed by the sulfanilamide-NAD reaction, while ammonium nitrogen (NH_4^+-N) was determined by the indophenol blue method followed by colorimetry. Soil available phosphorus (available P) was extracted by an acid-ammonium fluoride solution, followed by colorimetry at 700 nm (Liu et al., 1996).

2.4 | SOC chemical composition measurement

The chemical compositions of SOC were measured by ^{13}C cross-polarization magic angle spinning (CPMAS) nuclear magnetic resonance (NMR). In brief, 8 g air-dried soil was pretreated with a hydrofluoric acid solution (HF) eight times as described in Mathers et al. (2003). The NMR signals were collected on an AVANCE III spectrometer (Bruker Ascend™ 300 WB, Bruker, Karlsruhe, Germany) as described in Zhang et al. (2017) with a minor modification of 12,000 scans. The area below each spectrum was integrated and separated into four different C functional groups based on their chemical shift values, including alkyl-C (0–50 ppm), O-alkyl-C (50–110 ppm), aromatic-C (110–160 ppm), and carbonyl-C (160–220 ppm) groups (Mao et al., 2000; Ono et al., 2011). Unfortunately, the soil C concentration in the BL was too low to obtain useful NMR signals.

2.5 | Determination of soil water-stable aggregates

Soil aggregates were measured by the wet sieve method according to Cambardella & Elliott (1993), dividing into four classes of particular sizes: <0.053 mm, 0.053–0.25 mm, 0.25–2.00 mm, and >2.00 mm with a grainsize analyzer (DM200-III, Damon, Shanghai, China). Briefly, a 200 g air-dried soil sample was gently placed on the first sieve (2.00 mm) and then capillary rewetted with distilled water and incubated for 5 min. The sieves were then placed into a bucket with pre-poured distilled water for mechanical wet sieving. The sieves oscillated at a frequency of 50 cycles per minute for 30 min. The materials on the sieves were washed gently into pre-weighed aluminum specimen boxes, dried at 105°C, and weighed after cooling down (Blaud et al., 2017). The mean weight diameter (MWD) was used to evaluate the stability of soil aggregates and was calculated as follows (Zhang & Horn, 2001):

$$\mathrm{MWD} = \sum_{n=1}^{n+1} \frac{r_{i-1} + r_i}{2} \times m_i,$$

Where: r_i is the aperture of the i_{th} mesh (mm), $r_0 = r_1$ and $r_n = r_{n+1}$; m_i is the fraction of aggregation remaining on the i_{th} sieve; and n is the number of the soil aggregate size fractions (representing <0.053 mm, 0.053–0.25 mm, 0.25–2.00 mm, and >2.00 mm).

2.6 | Determinations of soil microbial biomass, arbuscular mycorrhizal fungal biomass, and diversity

Soil microbial and AMF biomass were characterized using the phospholipid fatty acid (PLFA) method as described in Frostegård & Bååth (1996) with minor modifications. Selected PLFA biomarkers were used to represent different soil microbes (Li et al., 2020) and the specific biomarker 16:1ω5 was used as the AMF biomarker (Zhang et al., 2020). Microbial and AMF biomass was calculated as nmol g^{-1} based on the internal standard (19:0) concentration. AMF diversity was analyzed by high-throughput sequencing on an Illumina HiSeq2000 platform as described in Zhang et al. (2021). AMF α-diversity was calculated by the Shannon-Wiener index. Nevertheless, the α-diversity could not be determined in the BL due to the low DNA concentration of AMF.

2.7 | Statistical analysis

Statistical analyses were conducted after all data (means ± SE, $n = 5$) had been checked for normal distribution and homogeneity. Using

SPSS 24.0 statistical software (IBM, Armonk, NY, USA), one-way ANOVA was applied to compare the significant difference ($p < 0.05$) in soil nutrient variables, GRSPs, soil aggregates, and soil C chemical compositions among different restoration treatments. Linear regressions were used to develop the relationship between the proportion of GRSP (GRSP/SOC) and the percentage of different soil C chemical groups, and between the concentrations of GRSP and SOC. Correlation analyses were used to test the relationship between GRSP and different soil aggregates.

3 | RESULTS

3.1 | Soil physicochemical properties, the concentrations of SOC and GRSP

The concentrations of soil total N, total P, NO_3^--N, NH_4^+-N, and available P were significantly increased as forest restoration progressed (Table 1). Similarly, the SOC concentration was also significantly enhanced with the vegetation restoration process. In particular, the SOC concentration in the forest restoration practices (EF, MF, and SF) was 5 to 13-times higher than that in the BL ($p < 0.05$, Figure 3a).

The EE-GRSP concentration ranged from 0.14 to 1.91 mg g^{-1} dry soil and was significantly increased by 3.9 to 12.3-times from EF to SF compared with the BL ($p < 0.05$, Figure 2a). Similarly, T-GRSP concentration also increased ($p < 0.05$) with forest restoration, and its highest concentration (7 mg g^{-1}) was found in the SF, which was 4.6-times higher than that in the BL (Figure 2a). The ratio of EE-GRSP to T-GRSP (EE-GRSP/T-GRSP, 0.1–0.3) increased from BL to MF ($p < 0.05$), whereas decreased slightly from MF to SF ($p > 0.05$, Figure 2b).

3.2 | Soil organic carbon chemical composition and aggregate stability

The ^{13}C NMR analysis showed that SOC had a relatively high percentage of O-alkyl-C (~40% of the total), alkyl-C (~32% of the total), and carbonyl-C (~22% of the total) groups, while the percentage of aromatic-C was relatively low (~5.02% of the total, Figure 3b) in all of these restoration sites. The percentage of the relatively easily degradable carbonyl-C was similar in all these restoration sites, and the percentage of the relatively easily degradable O-alkyl-C was higher in the MF than in other restoration treatments. However, the relative percentages of the recalcitrant alkyl-C and recalcitrant aromatic-C were highest in the SF and EF, respectively (Figure 3b).

The proportion of large macroaggregates (> 2 mm) increased, whereas the proportions of other aggregate sizes (0.25–2 mm, 0.053–0.25 mm, and <0.053 mm) decreased with the forest restoration ($p < 0.05$, Table 2). Significantly greater aggregate stability among restoration treatments ranked as SF ≈ MF > EF > BL based on the MWD values (Table 2). Among different aggregate sizes for the same forest restoration treatment, significantly greater aggregate proportions were ranked in descending order as 0.25–2 mm > 0.053–0.25 mm > (<0.053 mm) ≈ (>2 mm) under BL, and as (>2 mm) > 0.25–2 mm > 0.053–0.25 mm ≈ (<0.053 mm) under EF, MF, and SF (Table 2).

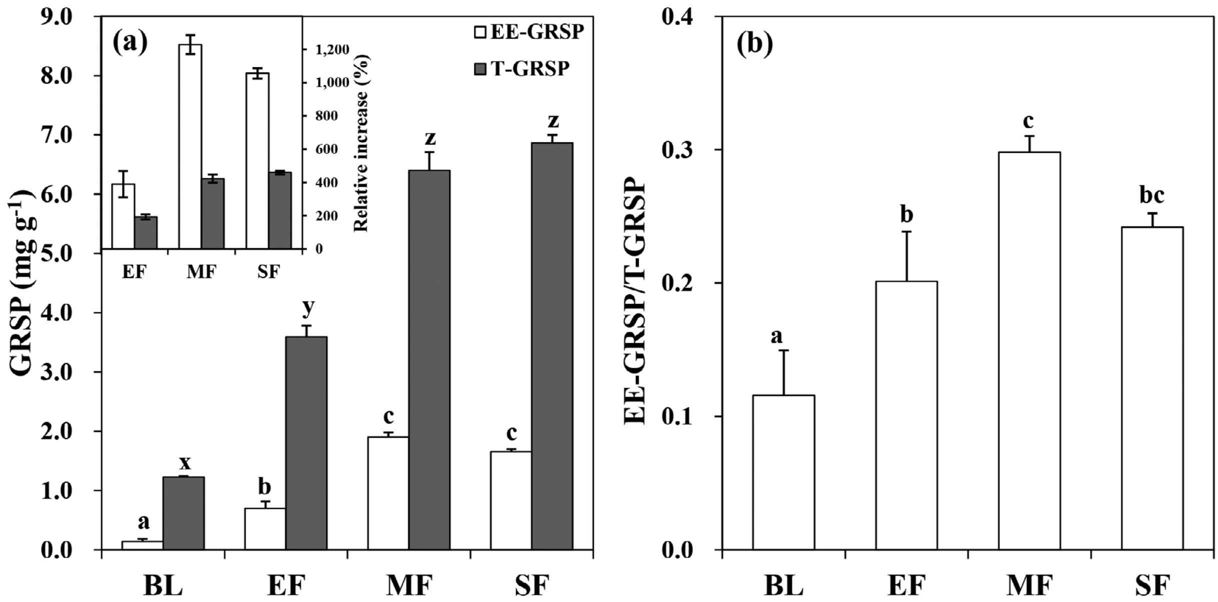

FIGURE 2 Easily extracted glomalin-related soil protein (EE-GRSP), total GRSP (T-GRSP), and the ratio of EE-GRSP/T-GRSP among the four study forest restoration practices. BL, barren land; EF, eucalyptus forest; MF, mixed broadleaved forest; SF, secondary natural forest. The insert plot is the relative increase of different restoration practices compared to the barren land. Different lower-cases represent significant differences among the forest restoration practices ($p < 0.05$)

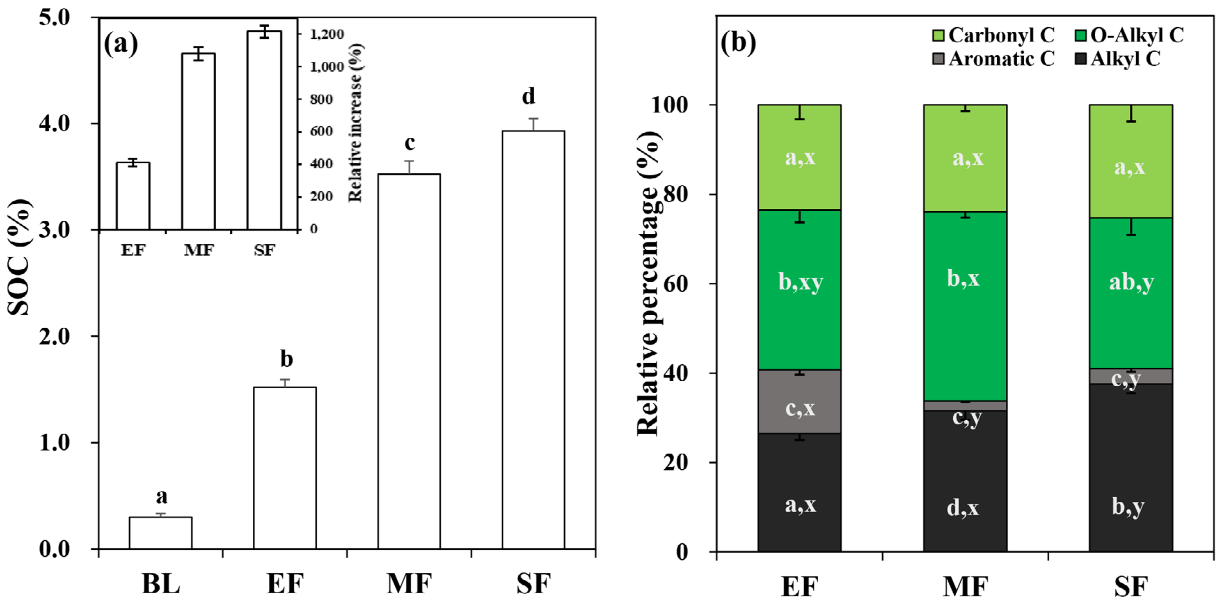

FIGURE 3 The concentrations of SOC (panel a) and the relative percentage of different soil chemical groups (panel b) among the four study forest restoration practices. BL, barren land; EF, eucalyptus forest; MF, mixed broadleaved forest; SF, secondary natural forest. The insert plot is the relative increase in restoration practices compared to the barren land. Different lower-case letters (a,b,c,d) represent the significant difference of different soil chemical groups in the same forest restoration practice ($p < 0.05$); while bars of the same colour in panel B sharing different letters (x,y,z) indicate the significant difference in the relative proportion of the same functional group among different forest restoration practices ($p < 0.05$). The soil carbon concentration in the BL was too low to obtain useful NMR signals [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 2 Soil aggregate relative proportion in the four study restoration sites and the correlations between the relative proportion of soil aggregates and GRSP content

	> 2 mm[†]	0.25–2 mm	0.053–0.25 mm	<0.053 mm	MWD
BL	9.24 ± 2.75 c,[‡]	52.19 ± 4.86 a,x	27.04 ± 0.97 a,y	12.54 ± 2.40 a,z	1.16 ± 0.13 c
EF	58.24 ± 5.63 b,x	23.79 ± 3.38 b,y	13.63 ± 1.95 b,yz	4.32 ± 0.66 b,z	3.78 ± 0.30 b
MF	79.03 ± 0.71 a,x	13.72 ± 2.44 cd,y	4.78 ± 0.97 c,z	2.46 ± 1.11 b,z	4.86 ± 0.05 a
SF	72.69 ± 2.01 a,x	22.36 ± 1.04 bc,y	3.95 ± 0.94 c,z	1.10 ± 0.16 b,z	4.62 ± 0.11 a
EE-GRSP	0.81**	−0.68**	−0.72**	−0.69**	0.89**
T-GRSP	0.72**	−0.66**	−0.83**	−0.75**	0.79**

Abbreviations: BL, barren land; EF, *Eucalyptus* forest; MF, mixed broadleaved forest; MWD, mean weight diameter; SF, secondary natural forest
[†]>2 mm, 0.25–2 mm, 0.053–0.25 mm and <0.053 mm are different soil aggregates size
[‡]a, b and c represent significant differences among the study forest restoration practices for the same aggregate size ($p < 0.05$), and x, y and z represent significant differences among aggregate sizes for the same forest restoration practice ($p < 0.05$). ** represent $p < 0.01$

3.3 | Relationships between GRSP and SOC, soil carbon chemical composition, and soil aggregate stability

Averagely EE-GRSP and T-GRSP accounted for 1.7% and 9.6% of SOC, respectively (Figure 4a), when 37% of C in GRSP (Lovelock et al., 2004) was adopted. There were no significant differences in the proportion of EE-GRSP to SOC among all of the vegetation restoration treatments (Figure 4a). The proportion of T-GRSP to SOC significantly decreased with forest restoration, and the lowest and highest proportions were found in the SF and BL, respectively (Figure 4a). Regression analyses showed that both EE-GRSP and T-GRSP had a strongly positive relationship with SOC ($p < 0.01$, Figure 4b). Both EE-GRSP and T-GRSP were significantly positively correlated with the proportion of large macroaggregates (>2 mm) and MWD, but significantly negatively correlated with aggregates with smaller particle sizes (0.25–2 mm, 0.053–0.25 mm, and <0.053 mm) (Table 2).

Different percentages of soil C chemical composition displayed different correlations with the ratio of GRSP to SOC (EE-GRSP/SOC and T-GRSP/SOC). Specifically, the percentage of the recalcitrant aromatic-C or recalcitrant alkyl C increased or decreased with the ratio of T-GRSP/SOC (Figure 5a,c), but neither of them exhibited any relationship to the ratio of EE-GRSP/SOC (Figure 5a,c). In addition,

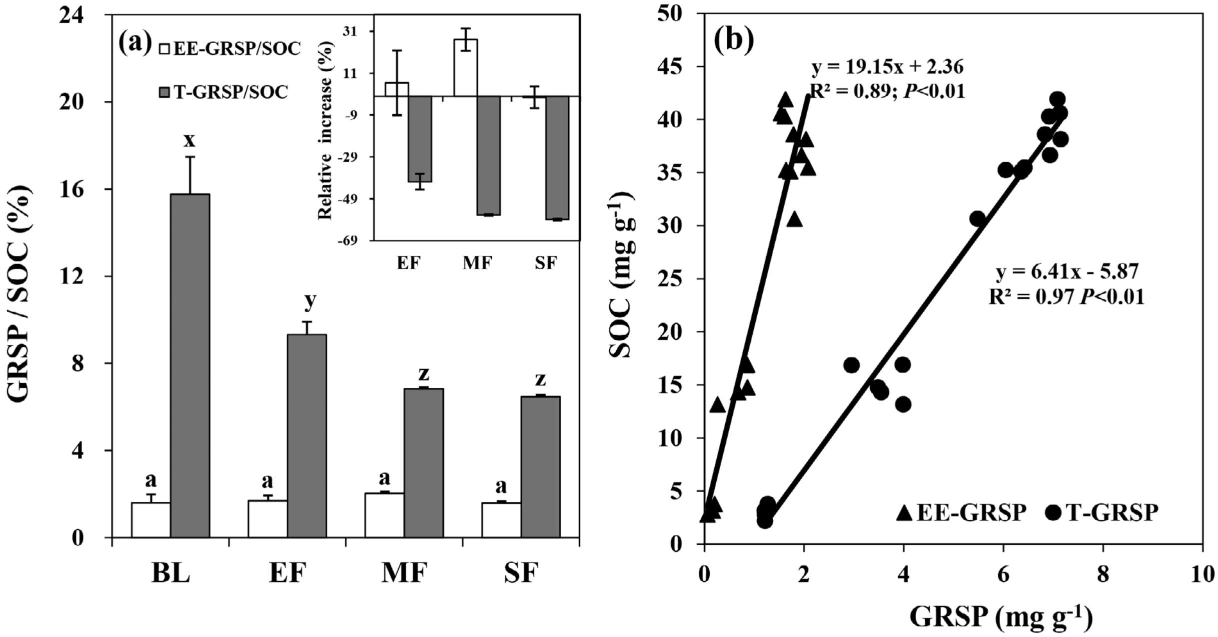

FIGURE 4 The proportion of EE-GRSP and T-GRSP in SOC among the four study forest restoration practices (panel a), and the relationship of EE-GRSP and T-GRSP to the SOC content (panel b). BL, barren land; EF, eucalyptus forest; MF, mixed broadleaved forest; SF, secondary natural forest. The insert plot is the relative increase in restoration practices compared to the barren land. Different lower-case letters above bars of the same filling colour represent significant differences among different forest restoration practices ($p < 0.05$)

neither the percentage of the easily degradable O-alkyl C nor carbonyl-C showed any significant relationship with the ratio of T-GRSP/SOC (Figure 5b,d).

4 | DISCUSSION

4.1 | Changes in GRSP concentration among the four study forest restoration practices

The increases of T-GRSP with forest restoration practices probably resulted from the tradeoff between the production of GRSP by AMF and the microbial decomposition of GRSP, because both the AMF and microbial biomass increased from BL to SF (Table 1). Specifically, only a few kinds of herbaceous plants and small xeric shrubs grew in the ditches in BL, where the topsoil had been completely eroded (Ren et al., 2007). Therefore, the degree of AMF colonization in the BL would not be intensive due to a scarcer root system over there. In contrast, AMF could be preserved and propagated by *E. exserta* in the EF since AMF can promote *E. exserta* growth (Adjoud et al., 1996). Similarly, AMF biomass increased in the MF and SF, as did GRSP (Table 1 and Figure 2a). The similar GRSP concentration under MF and SF partly revealed that the restoration was effective after 40 years of plantation with mixed broadleaved tree species after the cutting down of *E. exserta* trees in the EF. This was in coincidence with previous studies, which showed that AMF increased with the increase of plant diversity and biomass production (Hiiesalu et al., 2014). It is also in line with the fact that higher GRSP was accumulated in forest soil than in herb or shrub soil (Singh et al., 2016; Singh et al., 2018). Soil microorganisms under MF and SF would prefer to use the easily decomposable soil organic matter rather than the relatively recalcitrant T-GRSP, although the decomposition rate could also be increased with restoration due to an increase of the total microbial biomass.

EE-GRSP is composed of the newly produced or readily decomposed GRSP in soil (Steinberg & Rillig, 2003). The increase of EE-GRSP could be attributed to the increased AMF (exuding more GRSP) because EE-GRSP was significantly correlated with AMF biomass (Figure S1) or the increased microbial biomass (more T-GRSP decomposed as EE-GRSP) with the progression of restoration (Table 1). The increased ratio of EE-GRSP/T-GRSP from BL to MF indicated that the restoration process increased the fraction of labile GRSP. However, the ratio of EE-GRSP/T-GRSP slightly decreased in the SF compared with MF (Table 1), which suggested that restoration climax could be beneficial for the sequestration of recalcitrant GRSP reserves. Considering the different stability of different fractions of GRSP, we speculate that although EE-GRSP and T-GRSP have already reached the maximum value under MF, it is probably still not enough for benefiting the reservation of the recalcitrant GRSP in this forest.

In this study, the increased AMF biomass could well explain the changes in GRSP during the forest restoration process because it significantly positively correlated with both EE-GRSP and T-GRSP (Figure S1). It should, however, be noted that although it is a good indicator of AMF biomass, the PLFA biomarker 16:1 ω5 also includes bacterial taxa (Ngosong et al., 2012). In addition, the AMF diversity increased with the forest restoration as the GRSP (Table 1), which supported our first hypothesis.

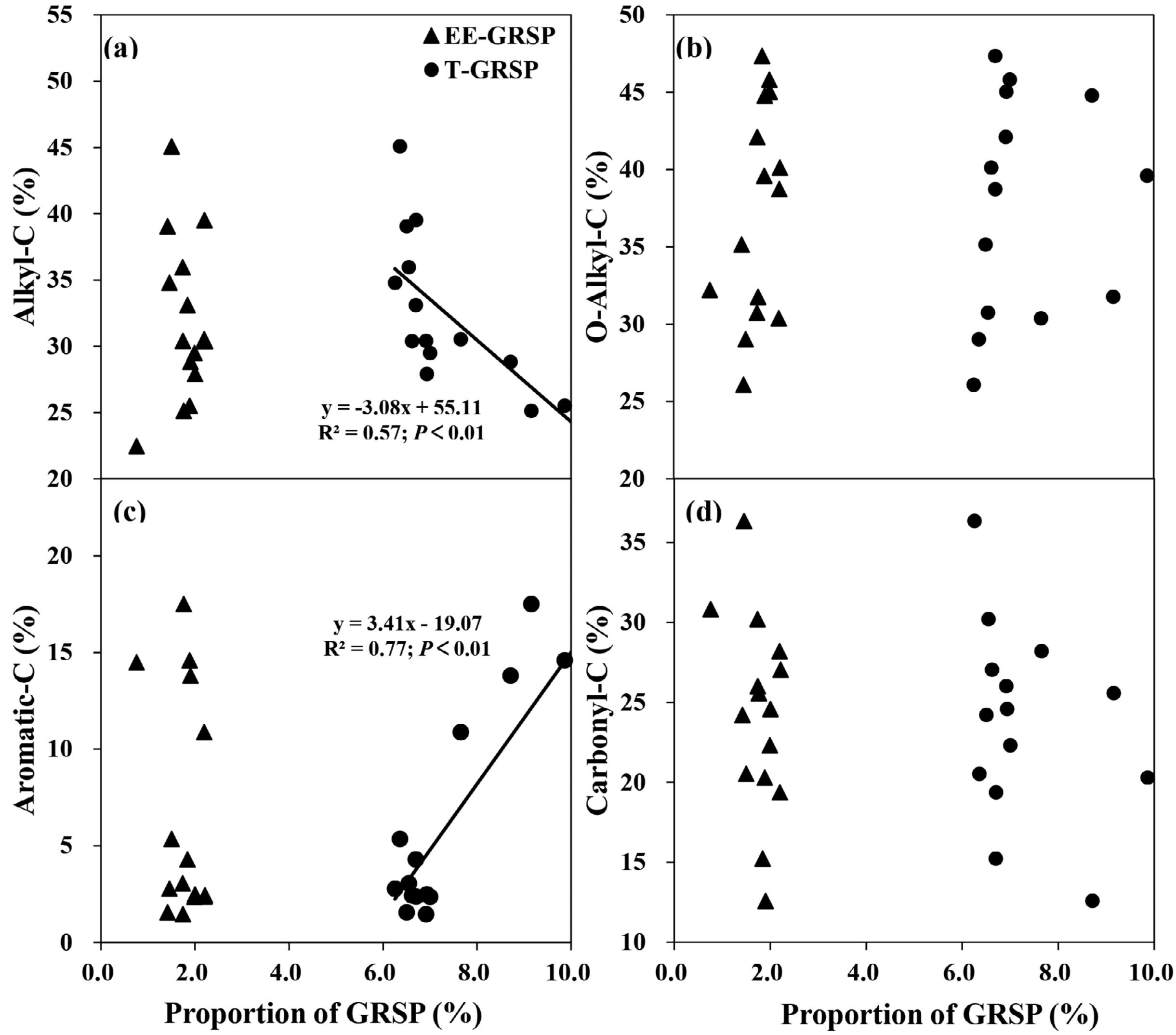

FIGURE 5 The correlation of the relative proportions of each soil chemical composition and the proportion of GRSP in SOC among the four study forest restoration practices. The trendline is present if significant ($p < 0.05$)

4.2 | Changes in soil organic carbon, chemical composition, and soil aggregates among the four study forest restoration practices

SOC significantly increased with forest restoration (Figure 3a), which is in line with previous studies (Li et al., 2012; Liu et al., 2018). The increase of SOC is mainly derived from the input of plant residues to the soil with restoration age (Post & Kwon, 2000). The similar SOC in the MF and SF restoration practices (Figure 3a) was in line with a meta-analysis result which showed that the secondary and primary tropical forest had a similar capacity to sequestrate SOC, because soil carbon in tropical forests can be accumulated rapidly and is resilient to land-use change (Martin et al., 2013). In addition, studies in the same site found that plant biomass and soil C sequestration capacity under MF and SF were comparable (Tang et al., 2018; Zhang et al., 2019). This was probably because the relevant C input and output were equally. Nevertheless, this aspect requires further study because we have only observed that soil microbial biomass (partly representing decomposition capacity, Table 1) in MF was comparable with that in the SF.

Soil MWD also increased with forest restoration (Table 2). The increased SOC and plant diversity was the possible underlying mechanism that improved soil aggregate stability in the process of vegetation restoration in this study area (Wei et al., 2013). Furthermore, the hyphae of AMF would facilitate the formation of soil aggregates (Morris et al., 2019), which was supported by our AMF diversity and biomass results (Table 1). These results indicated that the restoration of vegetation could improve the formation and stabilization of soil macroaggregates, and hence, improve the stability of soil structure and soil C storage.

The solid-state ^{13}C NMR spectra of SOC showed a similar recalcitrant C percentage (aromatic-C + alkyl-C) in the EF and SF (Figure 3b). The reasons for the relatively higher recalcitrant C percentages in the EF and SF were different because the aromatic-C in the EF was higher than in the other two restoration practices, whereas the SF had a higher proportion of alkyl-C than the other two forests (Figure 3b). In the EF, the rich aromatic-C probably derived from the eucalyptus leaves because they were rich in aromatic hydrocarbon, as a large amount of aromatic-C could be returned to the soil through fallen leaves (Rodriguez et al., 2012). In contrast, SF had the highest microbial biomass among all of the restoration sites (Table 1). As soil microorganisms would prefer to use labile C rather than the resistant components, the recalcitrant C could be deposited and gradually sequestrated in soil. Our results were also supported by the results of SOC density fractionation analysis, which showed that the proportions of recalcitrant C in the EF and SF were higher than that in the MF (Zhang et al., 2019). As a result, the SF and the EF could enhance the ratio of soil recalcitrant C fractions and thus benefit soil C sequestration.

4.3 | Relationships between GRSP and SOC sequestration among the four study forest restoration practices

The higher ratio of T-GRSP/SOC in the BL and the EF than in the MF and SF (Figure 4a) did not support our second hypothesis. This lower ratio in the MF and SF was caused by more proportional increases in SOC than in T-GRSP as shown in the insert plot in Figures 2a and 3a. The disproportionate increase of T-GRSP and SOC in different restoration practices could attribute to the fact that the turnover of GRSP was slower than that of SOC because the recalcitrant index of SOC was significantly lower than that of GRSP (Zhang et al., 2017), and the SOC concentration was higher under MF and SF than under BL and EF (Figure 3a). However, there were insignificant differences in the ratio of EE-GRSP to SOC (EE-GRSP/SOC) between different restoration practices (Figure 4a), which might be due to a similar increase in the magnitude of EE-GRSP and SOC among all of the restoration practices (Figures 2a and 3a). Furthermore, the positive correlation between GRSP and SOC (Figure 4b) was in line with studies in grasslands (Zhang et al., 2020) and subtropical forests (Zhang et al., 2017). The increase of GRSP but the decreased percentage of GRSP in SOC in the forest restoration process suggest that GRSP was more important for SOC accumulation in the earlier forest restoration practices.

The positive correlations between the ratio of GRSP/SOC and the aromatic-C percentage (Figure 5c) revealed that GRSP was probably related to the recalcitrant C sequestration at our restoration sites as aromatic-C was enriched in GRSP (Zhang et al., 2017). The percentage of the alkyl-C in GRSP was comparable or significantly lower than that in SOC (Zhang et al., 2017), which partly explains why there was a negative correlation between the ratio of T-GRSP/SOC and alkyl-C percentage (Figure 5a). Moreover, our results showed that EE-GRSP and T-GRSP were significantly positively correlated with large macroaggregates (> 2 mm) and MWD (Table 2). These findings were consistent with the results from a path analysis that indicated that GRSP significantly promoted water-stable aggregates in a grassland in California (Rillig et al., 2002). Miller and Jastrow (2000) also suggested that most of the increase in large macroaggregates was due to the binding of small particles into macroaggregates by GRSP. GRSP functions as a 'super glue' and forms a ‘sticky-string-bag’ with the mycelia of AMF, making them important for soil structure in the long term (Rillig, 2004; Wright & Upadhyaya, 1998). In addition, GRSP promoted soil aggregate formation and benefited SOC accumulation because it provided physical protection from microbial degradation for labile C within aggregates (Rillig, 2004). In summary, the accumulation of GRSP would be beneficial to the soil C sequestration in the tropical coastal degraded forest ecosystem restoration process, as in other natural and agricultural ecosystems (Liu et al., 2018; Wright et al., 2007).

5 | CONCLUSION

Restoration of barren lands significantly increases the concentration of GRSP because of the increase of AMF biomass and diversity after decades of reforestation. Accompanied by the accumulation of GRSP, forest restoration also improved the soil aggregate stability and proportion of soil recalcitrant C fractions. GRSP probably plays a more important role in SOC accumulation in the single species forest than in the multispecies community because the concentration of GRSP increased, but the ratio of GRSP to SOC decreased with forest restoration. GRSP could be beneficial to soil C sequestration by increasing the proportion of recalcitrant C components and soil aggregate stability. Given the important role of GRSP in SOC sequestration, our results provide a specific restoration strategy to improve degraded coastal lands. Specifically, we can inoculate AMF or plant-AMF hybrid plantations (plants that are colonized by AMF) to improve soil physical stability and SOC sequestration.

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CONFLICT OF INTEREST

The authors declare that they do not have a conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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