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Spatial distribution of glomalin-related soil protein and its relationship with sediment carbon sequestration across a mangrove forest

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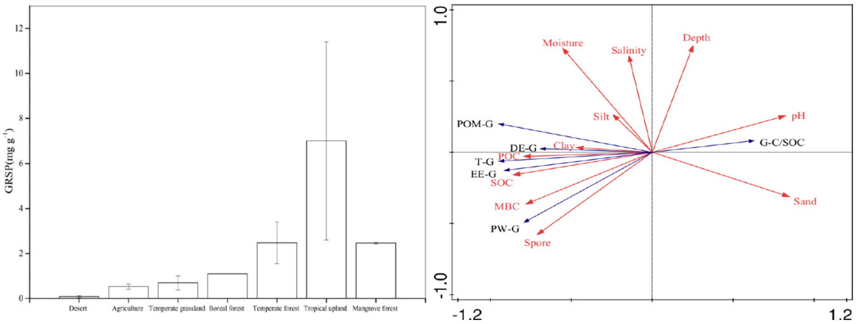
HIGHLIGHTS

- Mean contents of GRSP were 2.07 ± 0.04 mg g^{-1}, accounting for approximately 3.9% of SOC, and its contribution could far exceed that of MBC in the 0-50 cm sediment layers.
- GRSP could be transported by pore water and accumulated in sediment profiles.
- The recalcitrant AM-specific glycoprotein offset the effects of mangrove carbon loss, especially labile C.
- Environmental factors had an important impact on the transfer and accumulation of GRSP.
- Indigenous AM fungal propagules and GRSP transfer affected the total pool size of GRSP in the mangrove ecosystem.

GRAPHICAL ABSTRACT



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ABSTRACT

Arbuscular mycorrhizal (AM) fungi produce a recalcitrant glycoprotein, (glomalin-related soil protein (GRSP)), which can contribute to soil carbon sequestration. Here we made a first study to characterize the spatial distribution of GRSP fractions in a mangrove forest at Zhangjiang Estuary, Southeastern China and to explore potential contributions of GRSP to sediment organic carbon (SOC) in this forest. We identified GRSP fractions in surface sediments, as well as those at a depth of 50 cm. The contents of easily extractable GRSP (EE-GRSP), total GRSP (T-GRSP), GRSP in particulate organic matter (POM-GRSP) and GRSP in pore water (PW-GRSP) ranged between 1.20–2.22 mg g^{-1}, 1.38–2.61 mg g^{-1}, 1.45–10.78 mg g^{-1} and 10.35–39.65 mg L^{-1} respectively, and these four GRSPs are significantly affected by sample sites and sediment layers. Carbon in GRSP accounted for 2.8–5.9% of SOC and its contributions can far exceed that of microbial biomass carbon (0.21–0.73%) in the 0–50 cm sediment layers. Our data indicate that GRSP could be transported by pore water and accumulated in sediment profiles. The non-linear regression analysis revealed that as SOC and particulate organic carbon (POC) contents decrease, GRSP proportions increase, indicating the increase of the recalcitrant carbon offsetting the effects of mangrove carbon loss, especially labile C. Regression and ordination analyses indicated that GRSP fractions were mainly positively correlated with sediment carbon fractions and spore density but were negatively correlated with sand, pH. Strikingly, the unfavorable environmental factors for microbial organisms, especially AM fungi, prove to be able to promote the production or accumulation of GRSP. We propose that there are two different pathways for affecting

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the pool size of GRSP in mangrove ecosystems: (i) directly via indigenous AM fungi propagules; (ii) or via the GRSP transport and deposition by pore water and tides.

1. Introduction

As a type of coastal woody vegetation that is adapted to saline coastal soils distributed along the tropical and subtropical regions, mangrove forests are known as highly productive ecosystems, as they can provide significant inputs of litterfall and can efficiently accumulate a range of other sources of suspended material (Alongi et al., 2005; Bouillon et al., 2004). As a consequence, mangrove forests are important carbon sinks and have one of the highest carbon stocks per area compared with the world's other major forest domains, such as tropical rain forests (Donato et al., 2011; Alongi, 2007). However, mangroves are architecturally simple compared with terrestrial forests, and are vulnerable to environmental threats (Lovelock et al., 2011). The areal extent of mangrove forests has declined by 30–50% over the past half century as a result of natural disturbances and human stressors (Duke et al., 2007; Polidoro et al., 2010). Disturbances of mangrove carbon stocks can result in significant changes in sediment characteristics and accelerate emission rates of greenhouse gases (GHGs), especially CO_2 (Lovelock et al., 2011). Whereas the elevated CO_2 increases the labile carbon contents (e.g., particulate organic carbon (POC)), the recalcitrant soil organic carbon does not (Schlesinger and Lichter, 2001; Chen et al., 2012). Meanwhile, changes of sediment physico-chemical properties have an influence on a variety of organisms, spanning various autotrophic and mixotrophic microbes (Sahoo and Dhal, 2009; Chen et al., 2016). Sediment microorganisms are important components of mangrove ecosystems and can assist in the decomposition of organic matter and are vital for the cycling of sediment carbon (Chen et al., 2016).

As one of the most important soil microbes, arbuscular mycorrhizal (AM) fungi could form symbiotic relationships with >80% of all plant species (Smith and Read, 2008). The fungi are thought to ameliorate a variety of biotic and abiotic stresses to the plants (Smith and Read, 2008). AM external hyphae can improve the growth of plants by increasing uptake of available soil phosphorus (P), in exchange for host plant photosynthetic products. They play a significant role in the global C cycle because they utilize an estimated 20% of photosynthetic carbon (Treseder and Allen, 2000; Smith and Read, 2008), forming a significant pathway to transfer mycorrhizal carbon to soils and store it in the soils in the long term (Clemmensen et al., 2013; Johnson et al., 2002).

Studies have indicated that most of the mangrove plant communities including *Avicennia marina*, *Kandelia obovata*, and *Aegiceras corniculatum* can be colonized with AM fungi, and found the presence of AM fungi in the aerenchymatous cortex that may be aiding in AM fungi survival by providing oxygen (Kothamasi et al., 2006; D'Souza and Rodrigues, 2013; Wang et al., 2011, 2015). AM fungi significantly improved mangrove plant species growth and increased absorption of N, P and K (Wang et al., 2010; Xie et al., 2014). Some studies demonstrated that mycorrhizal colonization and spore density in the rhizosphere of mangroves were influenced by salinity level, host plant species and hydrological conditions (Wang et al., 2011; Kumar and Ghose, 2008; Kothamasi et al., 2006). It has been reported that AM fungi can contribute to soil carbon sequestration by immobilizing carbon in living mycorrhizal tissues, and by producing a specific recalcitrant glycoprotein, namely glomalin (Treseder et al., 2007; Lovelock et al., 2004). Glomalin is a structural component of hyphae and the spore wall and is released into the soil with fungal senescence and microbial decomposition (Wright and Upadhyaya, 1996, 1998). The AM-specific glycoprotein extracted from diverse soils has not been biochemically defined, but is operationally quantified and tagged as a glomalin-related soil protein (GRSP) (Rillig, 2004). GRSP has been found in multiple ecosystems, including agricultural lands, grasslands, forests, deserts, and non-cultivated soils (Treseder and Turner, 2007; Singh et al., 2013). Distribution of GRSP may provide insights into the importance of AM fungi and their products in sediment carbon sequestration in the mangrove ecosystem. Here we characterize GRSP contents in sediments across mangrove forest sites and mudflats within the 2360 ha of nature forest at Zhangjiang Estuary, Southeastern China.

Recently, the total GRSP has been categorized into two fractions, i.e., easily extractable GRSP (EE-GRSP) and difficultly-extractable GRSP (DE-GRSP), using operationally defined ease of extraction in citrate with autoclaving (Cornejo et al., 2008; Koide and Peoples, 2013; Wu et al., 2014). EE-GRSP is considered as the newly produced fraction, and is relatively more labile, whilst DE-GRSP represents the older fraction that is relatively stable (Wu et al., 2014). Most of the available information concerning GRSP fractions has been collected in relation to its role in soil aggregates in various soil types (Wright and Upadhyaya, 1998; Rillig et al., 1999; Rillig et al., 2003; Wu et al., 2014). Furthermore, GRSP contains substantial carbon and is accumulated in the soils, where it accumulates until it represents up to 5% of soil organic carbon (Rillig et al., 2001; Lovelock et al., 2004; Zhang et al., 2015). However, knowledge of contributions of GRSP to mangrove carbon pools remains largely unknown. The accumulation of GRSP in soil is dependent on numerous factors including AM fungi richness, plant community composition, land use systems and soil properties (Treseder and Turner, 2007; Singh et al., 2016). Compared with terrestrial ecosystems, the factors in mangrove ecosystems affecting the distribution and accumulation of GRSP are more complex. GRSP could be transported by rivers and groundwater, and mangroves, salt marsh, seagrass meadows, and coral reefs accumulate it in wetland ecosystem (Harner et al., 2004; Adame et al., 2010, 2012). Pool size of GRSP is thus enlarged, due to import from other terrestrial sources. In this study we analyze the pool sizes of different GRSP fractions, to make a preliminary assessment of the relative contributions of EE-GRSP, DE-GRSP, and GRSP in the particulate organic matter to total pool of GRSP in sediments. In addition, we measure the carbon content in GRSP (GRSP-C) to calculate its contributions to mangrove carbon pool and compare its contributions with those of other soil carbon pools, such as microbial biomass carbon (MBC).

Using core sediment samples collected from four sites in a mangrove forest at Zhangjiang Estuary, Southeastern China, the present study attempts to test the following hypotheses: (i) GRSP would be present in different sediment depths in mangrove forests. Because GRSP has been identified in multiple ecosystems (Rillig et al., 2001; Lovelock et al., 2004; Zhang et al., 2015) and a number of mangrove species associate with AM fungi. (ii) GRSP could be transported and deposited in sediment profiles. Because GRSP may enter rivers, groundwater and suspended solid in the coastal ecosystems (Harner et al., 2004; Adame et al., 2010, 2012), we expected GRSP would be transported to the mudflat that if it did enter pore water. (iii) GRSP could be a significant component of the mangrove C pool and is influenced by environmental factors. Because GRSP is a substantial contributor to soil carbon and the glycoprotein can modify a sub-optimal growth environment (Rillig and Steinberg, 2002).

2. Materials and methods

2.1. Site description

The study was conducted in Zhangjiang River Estuary Mangrove National Natural Reserves, which runs into Dongshan Bay, Fujian province,