



# Glomalin-related soil protein responses to elevated CO<sub>2</sub> and nitrogen addition in a subtropical forest: Potential consequences for soil carbon accumulation



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## ABSTRACT

According to the economy theory, plants should preferentially allocate photosynthate to acquire below-ground resources under elevated atmospheric carbon dioxide (eCO<sub>2</sub>) but decrease below-ground C allocation when nitrogen (N) is sufficient for plant growth. Arbuscular mycorrhizae (AM) represent a critical mechanism of below-ground nutrient acquisition for plants. The dynamics of arbuscular mycorrhizal fungi (AMF) could therefore reflect the response of plant C allocation under eCO<sub>2</sub> and N addition. We examined the responses of glomalin-related soil protein (GRSP) to eCO<sub>2</sub> (approximately 700 μmol mol<sup>-1</sup> CO<sub>2</sub>) and/or N addition (100 kg N ha<sup>-1</sup> yr<sup>-1</sup> as NH<sub>4</sub>NO<sub>3</sub>) in a modeled subtropical forest to better understand its potential influence on soil C storage. We hypothesized that GRSP would increase under eCO<sub>2</sub> and decrease under N addition. Furthermore, the positive effects of eCO<sub>2</sub> on GRSP would be offset by extra N addition, and GRSP would remain unchanged under combined eCO<sub>2</sub> and N addition. Our results showed that the mean concentrations of easily extractable GRSP (EE-GRSP) and total GRSP (T-GRSP) were 0.35 ± 0.05 and 0.72 ± 0.13 mg C cm<sup>-3</sup>, respectively, which accounted for 2.76 ± 0.53% and 5.67 ± 0.92% of soil organic carbon (SOC) in the 0–10 cm soil layer. Elevated CO<sub>2</sub> significantly increased T-GRSP by 35.02% but decreased EE-GRSP by 5.09% in the top 10 cm soil layer. The opposite responses of T-GRSP and EE-GRSP to eCO<sub>2</sub> might result from an unchanged photosynthate investment to AMF with possible changes in their decomposition rates. The effect of N on GRSP was contrary to our hypothesis, i.e., there was a 1.72%–48.49% increase in T-GRSP and a slightly increase in EE-GRSP. Both EE-GRSP and T-GRSP concentrations increased under the combination of eCO<sub>2</sub> and N addition, which was inconsistent with our hypothesis. The significant increase of EE-GRSP under the combination of eCO<sub>2</sub> and N addition was partly caused by more rapid plant growth and reduced microbial diversity, and the marginal increase of T-GRSP indicated that the interaction between eCO<sub>2</sub> and N addition offset their independent effects. In addition, the relatively higher accumulation ratios of GRSP (22.6 ± 13.6%) compared with SOC (15.9 ± 9.4%) indicated that more rapid GRSP deposition in the soil might accelerate SOC accumulation under eCO<sub>2</sub> and N addition. Our results will improve the understanding of the functioning of GRSP in soil C sequestration under global environmental change scenarios.

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## 1. Introduction

Human activities have induced environmental changes, such as elevated atmospheric carbon dioxide (CO<sub>2</sub>) concentrations and nitrogen (N) deposition. These changes affect C and N cycling in terrestrial ecosystems due to corresponding alterations of plant photosynthetic patterns and soil C pools (IPCC, 2014). For instance,

soil organic carbon (SOC) increased in a modeled subtropical forest because of enhanced tree growth under elevated CO<sub>2</sub> and N addition (Liu et al., 2010), whereas the elevated CO<sub>2</sub> and N addition increased the labile but not the recalcitrant SOC (Chen et al., 2012). In addition, increased N deposition influences soil microbial activities (Glaser et al., 2006; Carney et al., 2007), alters microbial community structure to the extent that the fungi: bacteria ratio is increased because of an increased fungal biomass (Liu et al., 2013), and hampers soil respiration (Deng et al., 2010). Numerous factors contribute to changes in SOC, including increased carbon input into the soil, decreased litter quality and decomposition rate, and the elevated protection of intra-aggregate or organic complexes (Treseder and Holden, 2013). However, little is known about the change in SOC composition under enhanced CO<sub>2</sub> and N addition (Sinsabaugh et al., 2004) because the origin and composition of soil organic matter are highly uncertain (Rillig et al., 2001b).

More than 80% of terrestrial vascular plant species are symbiotically associated with arbuscular mycorrhizal fungi (AMF) (Smith and Read, 2008). AMF play a crucial role in the global C cycle because they utilize approximately 20% of net plant photosynthates, deposit slow-cycling organic compounds such as chitin and glomalin into soils (Smith and Read, 2008; Wilson et al., 2009), and protect organic matter from decomposition by promoting the formation of soil aggregates (Wright and Upadhyaya, 1998; Rillig et al., 2002). <sup>13</sup>C<sub>2</sub>O<sub>2</sub> labeling in grassland demonstrated a rapid C flux from AM mycelia to soil (Johnson et al., 2002; Clemmensen et al., 2013). Whether mycorrhizal fungi promote C accumulation is determined by the sum of three processes: deposition of mycorrhizal residues, decomposition by mycorrhizal fungi, and increased plant growth (Treseder and Holden, 2013). Glomalin or glomalin-related soil protein (GRSP), which is a product of AMF that is deposited into soil after the hyphae senesce (Treseder and Turner, 2007), accounts for 4–5% of soil C, which exceeds the 0.08%–0.2% contribution by soil C from soil microbial biomass (Rillig et al., 2001b). In addition, the sticky nature of GRSP enables it to protect labile SOC through the formation of soil aggregates (Rillig et al., 2003; Rillig, 2004; Wu et al., 2014).

GRSP is usually categorized into two fractions, i.e., easily extractable GRSP (EE-GRSP) and total GRSP (T-GRSP), using assay methods (Wright and Upadhyaya, 1996). EE-GRSP is considered as the newly produced or nearly decomposed fraction, and T-GRSP represents the older fraction that is relatively stable (Wright and Upadhyaya, 1996; Rillig, 2004). The response of GRSP to elevated CO<sub>2</sub> or N depends on the ecosystem (Treseder and Turner, 2007), treatment period (Treseder, 2004), and treatment method (Garcia et al., 2008). Under elevated CO<sub>2</sub>, GRSP increased in grassland (Rillig et al., 1999, 2000; Vodnik et al., 2008), farmland (Rillig et al., 2001a) and steppe (Rillig et al., 2003) but not in a temperate forest (Garcia et al., 2008). Nitrogen addition promoted GRSP in a temperate forest (Garcia et al., 2008) and a tallgrass prairie (Wilson et al., 2009) but not in young boreal forests (Treseder et al., 2007). In addition, the combination of CO<sub>2</sub> and N insignificantly increased GRSP compared with the addition of N alone (Garcia et al., 2008). Various responses of GRSP to enhanced CO<sub>2</sub> and N addition occur largely because of the diversity of ecosystems studied, soil properties, species category, productivity and AM hyphae turnover rate (Rillig et al., 1999, 2000; Treseder, 2004; Treseder and Turner, 2007; Treseder et al., 2007). Moreover, most of the manipulated experiments were conducted in grasslands, farmlands and pot studies, and consequently, the combined effect of CO<sub>2</sub> enrichment and N addition on GRSP in subtropical forests remains largely unknown.

In this study, we examined GRSP concentrations in modeled typical subtropical forests that had been continuously exposed to elevated CO<sub>2</sub> and N addition for approximately 5.0 years from April 2005 to January 2010. Previous studies in these modeled forests

showed that elevated CO<sub>2</sub> enhanced plant growth (Zhao et al., 2011) and belowground biomass accumulation (Zhao et al., 2011; Yan et al., 2014). In addition, CO<sub>2</sub> enrichment facilitated C sequestration in soils (Liu et al., 2010), whereas extra nitrogen input was required for increased soil C accumulation even though the background N deposition was high (Fang et al., 2006). SOC fraction analyses indicated that elevated CO<sub>2</sub> increased the amount of labile SOC (e.g., particulate organic carbon (POC) and readily oxidizable organic carbon (ROC); Chen et al., 2012). Further, elevated CO<sub>2</sub> accelerated soil organic matter decomposition due to an increase in the soil respiration rate (Deng et al., 2010). However, as the 'super glue' in soil and a component of the soil C pool (Rillig et al., 2002), the role of GRSP was not addressed in these studies. Here, we tested three hypotheses regarding GRSP under elevated CO<sub>2</sub> and/or N addition. First, we hypothesized that both EE-GRSP and T-GRSP would be increased under elevated CO<sub>2</sub> because a more rapid aboveground plant growth could result in a higher allocation of photosynthates to belowground mycorrhizae. Second, we expected that under external N addition both fractions of GRSP would decline because plants might allocate less C to acquire nutrients from the soil. Third, we predicted that the combined effect of elevated CO<sub>2</sub> and N addition would not affect GRSP because the positive effect of CO<sub>2</sub> enrichment would be offset by the negative effect of the N supplement. The results should improve our understanding of the functioning of GRSP in soil C sequestration under global environmental change scenarios.

## 2. Materials and method

### 2.1. Study site

The study site was located in South China Botanical Garden, Chinese Academy of Sciences, Guangzhou, China (23°20' N and 113°30' E), which has a typical subtropical monsoon climate (hot-wet season from April to September and cool-dry season from October to March). The mean annual temperature is 21.9 °C, and the annual precipitation is 1750 mm (>80% in the hot-wet season). Nitrogen deposition in this region is 30–70 kg N ha<sup>-1</sup> year<sup>-1</sup> currently and may reach 100 kg N ha<sup>-1</sup> year<sup>-1</sup> in 2030 (Fang et al., 2006).

### 2.2. The modeled forest

Ten 3 m diameter open-top chambers (OTC; 0.7 m buried belowground and 3–4.5 m adjustable aboveground) were used to model the subtropical forest ecosystem. The aboveground section of the chambers was wrapped with transparent and impermeable plastic sheets, whereas the belowground section was cemented to prevent the movement of water and/or elements. Soil (an Udult subgroup within Ultisol, USDA classification) was collected from a nearby evergreen broad-leaved natural forest at depth of 0–20, 20–40 and 40–70 cm, and the samples were homogenized separately and then used to fill the belowground chambers (Liu et al., 2008). The soil had a pH of 4.2 and rich humus in the surface layer. The SOC, N and phosphorus contents were 16.33 ± 3.42, 0.52 ± 0.15, and 0.30 ± 0.09 g kg<sup>-1</sup>, respectively, for the top 0–20 cm (Liu et al., 2008). In March 2005, eight 1- to 2-year-old seedlings of six species (*Acmena acuminatissima* (Blume) Merr. et Perry, *Castanopsis hystrix* Hook.f. & Thomson ex A. DC, *Ormosia pinnata* (Lour.) Merr., *Pinus massoniana* Lambert, *Schima superba* Gardn. and *Syzygium hancei* Merr. et Perry) with similar basal diameter and height were randomly planted in each chamber. These six native species are widely spread throughout subtropical China. However, *P. massoniana* died in the second year due to competitive exclusion by other species.

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