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REVIEW ARTICLE

Glomalin: an arbuscular mycorrhizal fungal soil protein

Pradeep Kumar Singh · Meenakshi Singh ·
Bhumi Nath Tripathi

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Abstract Glomalin is abundant in soils and is closely correlated with aggregate water stability. Glomalin contains carbon and, hence, constitutes a non-trivial portion of the terrestrial carbon pool. Possibly far more importantly, however, stabilization of aggregates amplifies the role of glomalin in soils because carbonaceous compounds are protected from degradation inside of aggregates. Increased atmospheric CO_2 can lead to increased production of glomalin because of the symbiotic association that exists between plants and producers of glomalin, arbuscular mycorrhizal fungi (AMF). Glomalin concentrations in soils are influenced by management practices, for example, in agroecosystems, further highlighting the role of this protein in carbon storage. Glomalin is an unusual molecule that has proven difficult to analyze biochemically due to its recalcitrance and complexity. Future research will be directed towards the elucidation of its structure and controls on its production.

Keywords Rhizosphere · AMF · Protein · Glomalin

Introduction

The rhizosphere may be defined as the "heart of the soil" as it is the zone under the direct influence of plant roots and with high populations of active microorganisms (Napoli et al. 2008). In the rhizosphere, plant roots influence microbial communities by depositing photosynthates into the rhizosphere, and organisms govern plant growth and development (Napoli et al. 2008). Although the rhizosphere was first described by Hiltner (1904), numerous studies have observed microbial and plant activities in the soil dating as far back as 400 million years (Khan 2005; Napoli et al. 2008). Rhizosphere soils are defined as soils adhering to plant roots even with a moderate shake (Phillips and Fahey 2008; Idris et al. 2009). It may be difficult to physically separate rhizosphere and bulk soils from their inherent biological, chemical, and physical characteristics (Vessey 2003; Barea et al. 2005; Hinsinger et al. 2005).

The association between plants and arbuscular mycorrhizal fungi (AMF) is one of the most important symbioses on earth, linking the root and the soil system (Koide and Mosse 2004). AMF symbiosis is possibly the oldest and the most abundant plant–microbe association on earth (Smith and Read 1997). AMF belong to the phylum Glomeromycota and order Glomales (Schubler 2001). Plants are important in soil aggregate formation and the role of AMF is as vital because AMF symbiosis influences plant physiology such as root-to-shoot ratio, nutrient content, and rhizodeposition. Plant effects on soil aggregate formation, to a large extent, are governed by AMF activities (Rillig et al. 2002; Rillig 2004a, b; Rillig and Mummey 2006; Hallett et al. 2009). By influencing the root system, AMF enhance the enmeshment and entanglement of soil particles by the plant roots and root hairs (Rillig and Mummey 2006). Roots are known to exert some pressure on soil particles, thereby aligning and binding the particles together to facilitate soil aggregate formation (Rillig and Mummey 2006; Hallett et al. 2009). AMF influence the amount of pressure applied by the plant root through their effects on root density and branching pattern (Rillig and Mummey 2006).

The rhizosphere has direct influence of plant roots and harbors different microorganisms, and the interactions between these organisms can either benefit or hinder plant growth and development (Barea et al. 2005). AMF are known to promote plant growth and development by increasing

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P. K. Singh (✉) · M. Singh · B. N. Tripathi
Department of Botany, Guru Ghasidas University,
Bilapsur 495 009 Chhattisgarh, India
e-mail: pksbotany@gmail.com

nutrient acquisition and alleviating stress conditions of plants (Koide and Mosse 2004; Barea et al. 2005), and improve soil structure, and play a crucial role in soil carbon (C) storage (Zhu and Miller 2003; Rillig and Mummey 2006). These roles of AMF have been linked with the production of a novel fungal substance, termed glomalin (Zhu and Miller 2003; Rillig 2004a, b).

What is glomalin?

Glomalin (Wright and Upadhyaya 1996) is a fungal protein (or protein class) that is operationally quantified from soil as glomalin-related soil protein. Glomalin was thought to be exuded by the living fungus (Wright and Upadhyaya 1996) until Driver et al. (2005) found that glomalin is only released by an AMF into the soil environment during hyphal turnover and after the death of the fungus. Glomalin, though still not biochemically defined, is an N-linked glycoprotein composed of 3 to 5 % N, 36 to 59 % C (Lovelock et al. 2004; Schindler et al. 2007), 4 to 6 % hydrogen, 33 to 49 % oxygen, and 0.03 to 0.1 % P (Schindler et al. 2007). Glomalin also contains 0.8 to 8.8 % Fe (Wright and Upadhyaya 1998; Rillig et al. 2001), which may be responsible for the reddish color of glomalin extracts (Wright and Upadhyaya 1998). Glomalin is a stable compound, insoluble in water and resistant to heat degradation (Wright et al. 1996). Because it is gluelike in nature and attaches to horticultural film and soil surfaces, glomalin is likely hydrophobic in its native state (Wright and Upadhyaya 1998, 1999). Apart from the Glomeromycota, no other fungal group produces this glycoprotein in significant amounts (Wright and Upadhyaya 1996).

Glomalin has been found in agricultural, grassland, forest, desert, and non-cultivated soils (Wright and Upadhyaya 1996; Rillig et al. 2003a; Nichols and Wright 2004; Antibus et al. 2006; Bai et al. 2009). Glomalin concentrations of over 100 mg g^{-1} of soil were recorded in tropical forest soils of Hawaii (Rillig et al. 2001) and values lower than 1 mg g^{-1} soil were obtained in soils of a desert ecosystem (Bai et al. 2009). Values up to 21 mg g^{-1} soil were obtained from woodland soils (Wright and Upadhyaya 1998). Although most of these findings are based on glomalin in the A horizon, both B and C horizons contain glomalin (Rillig et al. 2003a) and it can be found to a depth of 140 cm in the soil profile (Harner et al. 2004). Harner et al. (2004) detected the glycoprotein in floodplain soils, river water, and river foam. In fact, river foam contained 9.66 mg g^{-1} of glomalin in freeze-dried foam.

Origin of glomalin

There are several significant problems in glomalin research; it should be made clear, though, that none of these problems pertain to the operational definition of glomalin *per se* but to the link between glomalin and AMF. In a complex medium such as soil, it is impossible to demonstrate that there are no other significantly cross-reactive substances present. Having a secondary specific detection system would clearly greatly enhance the confidence in the association between glomalin and AMF (Rillig 2004b). There is increasing circumstantial evidence accumulating from decomposition studies that glomalin is of AMF origin. When AMF growth is eliminated, e.g., by incubating soil without host plants, glomalin concentrations decline, along with AMF hyphae (Steinberg and Rillig 2003). Glomalin is deposited within the soil, where it accumulates until it represents as much as 5 % of soil C and N (Rillig et al. 2003a; Lovelock et al. 2004). The ecophysiological function of glomalin is unknown, although Gadkar and Rillig (2006) have found evidence that glomalin may be related to a heat shock protein.

Extractions and quantifications of glomalin

Glomalin is defined by the method employed to quantify it (Wright et al. 1996; Rillig 2004b). Bradford protein analysis is a common method for protein quantification (Bradford 1976). The Bradford assay is based on the principle that a dye (Coomassie Brilliant Blue G-250) binds with proteins and changes the dye color from red to blue (Bradford 1976; Wright et al. 1996). The degree of color change, read by a spectrophotometer at a wavelength of 590 nm (A590) as optical density, can be related to protein concentration in a glomalin extract using a standard of known concentration of protein. The standard is prepared in a range of 1.25 to 5 μg bovine serum albumin (BSA) in phosphate-buffered saline (PBS). The equation of the regression line generated by plotting optical density against BSA values is then used to calculate protein concentration in glomalin extracts as Bradford-reactive soil protein (BRSP) for total glomalin (TG) and easily extractable Bradford-reactive soil protein (EE-BRSP) for the easily extractable glomalin (EEG) fraction (Rillig 2004b).

TG quantified using ELISA is regarded as immunoreactive soil protein (IRSP) and the easily extractable fraction is named easily extractable immunoreactive soil protein (EE-IRSP) (Wright and Upadhyaya 1998; Rillig 2004b). Rillig (2004b) explained these terminologies (EE-BRSP, BRSP, EE-IRSP, and IRSP) in his review and cautioned against the use of the word glomalin to describe the soil fraction of glomalin. The extraction procedure does not eliminate other soil proteins. EE-BRSP and T-IRSP were positively correlated with soil available N and P (Wu et al. 2011). Rillig (2004b) suggested glomalin-related soil protein (GRSP) to be used instead, which is widely accepted. Table 1, modified from Rillig (2004b), describes each term

Table 1 Current terminologies for glomalin and their definitions (modified from Rillig 2004b)

Terminology	Description
Glomalin	A yet to be identified putative gene product of arbuscular mycorrhizal fungi
Glomalin-related soil protein (GRSP)	Total soil glomalin fraction, possibly contains other soil protein; fraction of soil glomalin extracted repeatedly using 50 mM sodium citrate solution (pH 8) and autoclaving at 121 °C for 60 min until glomalin extract is straw-colored
Easily extractable glomalin-related soil protein (EE-GRSP)	Fraction of soil glomalin extracted once using 20 mM sodium citrate solution (pH 7) and autoclaving at 121 °C for 30 min
Bradford-reactive soil protein (BRSP)	Glomalin-related soil protein quantified using the Bradford assay; measures all protein in glomalin extract
Easily extractable Bradford-reactive soil protein (EE-BRSP)	Easily extractable glomalin-related soil protein quantified using the Bradford assay; measures all protein in glomalin extract
Immunoreactive soil protein (IRSP)	Glomalin-related soil protein quantified using an indirect enzyme-linked immunosorbent assay (ELISA) with monoclonal antibody MAb32B11, specific for glomalin, though may cross-react with other soil protein
Easily extractable immunoreactive soil protein (EE-IRSP)	Easily extractable glomalin-related soil protein quantified using an indirect enzyme-linked immunosorbent assay (ELISA) with monoclonal antibody MAb32B11

to ensure clarity. In addition, some fractions of glomalin extracted from other sources (e.g., the root) would have similar terms. For instance, glomalin extracted from plant roots using the Bradford assay is Bradford-root protein (Rosier et al. 2008). Carbon in GRSP make a large contribution to the total organic C and give better soil structure and alter soil moisture retention properties to lead to better plant drought resistance and plant production (Wu et al. 2012).

Characterization of glomalin

Glomalin extracted from soil is very similar to glomalin extracted from single-species pot cultures. Samples have been examined using SDS-PAGE (Rillig et al. 2001; Wright et al. 1996; Wright and Upadhyaya 1996); NMR (Rillig et al. 2001); capillary electrophoresis (CE) (Wright et al. 1999); and C, H, N analysis by combustion (Rillig et al. 2001). There are minor variations in elemental constituents of glomalin among samples, but CE and SDS-PAGE demonstrated that glomalin extracted from soil is similar to glomalin from hyphae. (Rillig et al. 2003b) and Steinberg and Rillig (2003) examined decomposition of glomalin following moist soil incubation in the dark at 18 °C. One of the incubation studies (Steinberg and Rillig 2003) showed that hyphal length declined by 60 % after 150 days of incubation while TG declined by 25 %, IRTG disappeared almost completely, EEG did not change, but IREEG increased fivefold. In the other study (Rillig et al. 2003b), the TG declined by 48 to 81 % and the EEG declined by 51 to 88 % after 413 days of incubation. Using ^{14}C data, Rillig et al. (1999) calculated a turnover time for glomalin of 7 to 42 years. However, the incubation studies suggest that a long-lived, recalcitrant glomalin fraction exists with a much longer turnover time.

Glomalin production

Production rates of glomalin can be estimated from short-term greenhouse studies that do not last long enough for glomalin pools to turn over markedly. Glomalin is not exuded by AMF hyphae but is instead contained within hyphal walls (Driver et al. 2005). As the AMF hyphae die and decompose, they are thought to leave a residue of glomalin in the soil (Treseder and Allen 2000). Thus, hyphal standing stocks, hyphal glomalin content, and hyphal turnover rate should each determine the rates at which glomalin is deposited in the soil. Production rates of glomalin are not always correlated with AMF abundance in soil. To estimate glomalin yields as a function of AMF hyphal length, Lovelock et al. (2004) used sand-filled in-growth cores that were incubated in tropical forest soils in Costa Rica and in corn and sand cultures at the USDA in Maryland. A number of mechanisms may be responsible for the lack of a correlation between AMF hyphal lengths and glomalin observed in these studies.

Standing stocks of glomalin in soil are determined by its production and decomposition (Fig. 1), and environmental conditions could affect the two fluxes independently (Rillig 2004b). AMF can display plasticity in the amount of resources that they invest in glomalin construction. Rillig and Steinberg (2002) demonstrated that soil texture influences the yields of glomalin. In a global survey of soil

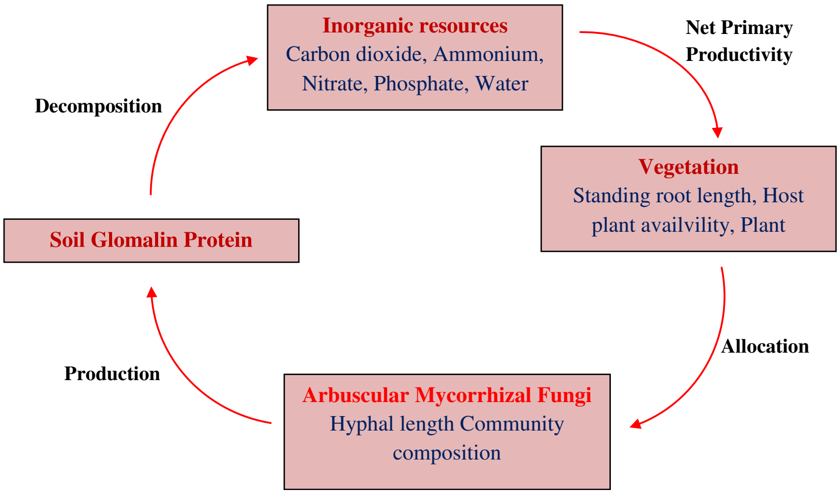

Fig. 1 Glomalin protein cycle in the ecosystem

glomalin concentrations, the variation among biomes relate glomalin stocks to net primary productivity (NPP) and AMF abundance. Both NPP and AMF are likely to influence glomalin production (Table 2).

Factors affecting glomalin production

Since the discovery that AMF are in symbiotic association with most plant species, it has been observed that the relationship is only completely mutual when AMF supply nutrients required by plant in exchange for plant C (Koide and Mosse 2004). The more dependent a plant is on mycorrhizal symbioses, the more C is allotted to AMF by the plant. In fact, plant C allocation to AMF can be up to 85 % for some plant species (Treseder and Allen 2000). Because a considerable amount of C allocated to AMF is used in glomalin production, plant productivity and photosynthate allocation will govern glomalin production by AMF (Treseder and Turner 2007). Plants are, therefore, a major determinant of glomalin production.

Violi et al. (2007) reported significant positive effects of plant growth rate and nutrient status on glomalin production. Rosier et al. (2008) related differences in glomalin-related protein (GRP) concentrations in the root of smooth brome (*Bromus inermis*), Sudan grass (*Sorghum bicolor*), and narrow leaf plantain (*Plantago lanceolata*) to length of the growth period and differences in host plant species. Under field conditions, the plant effect may be more pronounced than those observed in controlled environments with single AMF or plant species (Treseder and Turner 2007). Wilson et al. (2009) reported the possible influence of plant biomass, biomass allocation, and litter quality and quantity on GRSP concentration. This may be attributable to the dependence of AMF on host plant abundance and NPP (Treseder and Turner 2007).

Cropping systems and land management practices affect GRSP levels (Wright et al. 2007). After a 3-year period of converting from ploughed tillage to no-till, Wright et al. (1999) detected substantial increases in GRSP concentrations. Even with the conversion from conventional tillage to no-till, GRSP levels in the studied soil were lower than levels in undisturbed grassland (Wright et al. 1999). Rillig

Table 2 Net primary productivity and glomalin concentrations of biomes

Biome	Range of net primary productivity (kg C m^{-2} $year^{-1}$)	Range of glomalin protein (g kg^{-1} soil)	References
Agricultural	0.07–0.50	0.32–0.71	Franzluebbers et al. (2000), Wright and Anderson (2000), Wuest et al. (2005)
Boreal forest	0.17	1.1	Treseder et al. (2004)
Desert	0.09–0.18	0.003–0.13	Bird et al. (2002), Rillig et al. (2003a), Treseder and Turner (2007)
Temperate forest	0.05–0.74	0.60–5.8	Knorr et al. (2003), Steinberg and Rillig (2003), Nichols and Wright (2005), Treseder and Turner (2007)
Temperate grassland	0.08–0.62	0.23–2.5	Rillig et al. (1999), (2002), Lutgen et al. (2003), Batten et al. (2005), Nichols and Wright (2005)
Tropical rainforest	0.73–0.76	2.6–13.5	Rillig et al. (2001), Lovelock et al. (2004), Treseder and Turner (2007)

et al. (2003b) also indicated lower GRSP concentrations in agricultural soils relative to native forest and afforested soils. Tillage reduces glomalin production and enhances its decomposition by decreasing vegetation and AMF abundance (Treseder and Turner 2007).

Role of glomalin in soil aggregation

The long-term effect of AMF on aggregate stabilization may partly be credited to glomalin production by the fungi (Rillig 2004a, b; Rillig and Mummey 2006). Wright and Anderson (2000) found a positive correlation between GRSP concentrations and soil aggregate water stability across a variety of soils under different cropping systems and management practices. Using the path analysis model, Rillig et al. (2002) showed that the direct effect of GRSP on aggregate stability was higher than the total (direct and indirect) effect of hyphae on soil aggregate stability, but similar to the total root effect. Since soil aggregation governs water, nutrient content, and gaseous exchanges in soil (Rillig and Mummey 2006), glomalin could play a crucial role in soil aeration and drainage, plant nutrient uptake, and productivity (Nichols and Wright 2004). AM fungal colonization, spore density, and glomalin have a distinct spatial distribution pattern, which is influenced by soil factors. Soil urease, available N, and organic carbon are principal soil factors affecting the distribution of AM fungi and glomalin (Guo et al. 2012). Therefore, the distribution pattern of AM fungi and glomalin can be useful to monitor desertification and soil degradation.

Role of glomalin in carbon storage

Glomalin facilitates soil C storage (Zhu and Miller 2003; Rillig 2004b). Rillig et al. (2001) found that glomalin accounted for 4 to 5 % of total C and N in Hawaiian soils and reported the contributions of the glycoprotein to total C were greater than microbial biomass C. Their observation may be due to the slow turnover rate of glomalin and its ability to accumulate in soil (Steinberg and Rillig 2003). Wilson et al. (2009) observed reductions in soil C and N content due to AMF suppression and related it to significant decreases in AMF hyphae and GRSP concentrations. They speculated that decreases in AMF hyphae and GRSP concentrations led to the losses of C and N protected in macroaggregates by reducing aggregate stabilization. Nevertheless, not much is known about the direct influence of glomalin on organic C storage, since most of its relation to C storage is by virtue of stabilizing aggregates (Feeney et al. 2004).

Role of glomalin in stress tolerance

Glomalin has been linked with heat shock protein 60 (*hsp60*), which are proteins produced by eukaryotic and prokaryotic cells when under environmental-related stress conditions, such as increased temperatures, pH change, and starvation (Gadkar and Rillig 2006; Purin and Rillig 2007). Using liquid chromatography–mass spectrometry, Gadkar and Rillig (2006) demonstrated that the amino acid sequences of glomalin are related to *hsp60*, thereby confirming the speculations by other studies (Rillig and Steinberg 2002; Driver et al. 2005) that glomalin may be serving a protective function for AMF as a stress-induced protein. Relating glomalin with heat shock protein clarifies how stress imposed by heavy metals may rapidly increase glomalin production by AMF and GRSP concentrations in polluted soils (Cornejo et al. 2008). Rillig and Steinberg (2002) demonstrated that glomalin production decreased as AM fungal growing space increased. Their study was the first to show that unfavorable growing conditions may enhance glomalin production by AMF. Thus, they argued that glomalin is produced by AMF for AMF use and functional roles of glomalin in soil are secondary (Purin and Rillig 2007) or coincidental. It is conceivable that glomalin performs a protective function in a living fungus, since AMF allocates many of its resources (mainly C and N) to glomalin production (Rillig and Steinberg 2002).

Role of glomalin in reduction of greenhouse gases

Through land use change, the agricultural sector has become a major contributor to global warming (Janzen 2004). Currently, the atmospheric concentration of CO_2 has risen above the 370 ppm predicted by Keeling and Whorf (2002), and higher levels have been speculated (IPCC 2001). Because CO_2 emissions from soil are mainly due to poor management practices that destroy the soil structure (Lal 2004), any practice that promotes aggregate formation and stabilization will reduce soil C losses. It is interesting to note that the desirable effects of minimum tillage on soil structure have been linked to higher glomalin concentrations in these aggregated soils (Wright and Upadhyaya 1998; Wright and Anderson 2000). The high amount of hyphae produced by AMF is correlated with significant increases in the aggregate stability of soils, modifying the soil's ability to mobilize nutrients, water content, as well as root penetration in soil and soil erosion potential (Treseder and Turner 2007). In this sense, mycorrhizal networks can create indefinitely large numbers of fungal linkages connecting together many plants in a community and suggests that AMF formation could be an important element in the plant succession of ecosystems and reduction of greenhouse gases.

Glomalin can contribute immensely in reducing the release of N_2O into the atmosphere. Apart from being a N pool (Nichols and Wright 2006), glomalin may diminish N losses by the indirect influence on nitrification and denitrification. For example, at saturation, a poorly aggregated soil becomes anaerobic, which stimulates denitrification. Apparently, management practices developed to reduce N_2O emissions will increase glomalin production. For example, minimizing N fertilizer and manure application will benefit mycorrhizal symbioses and thus increase glomalin production and its beneficial roles in soil (Treseder and Turner 2007). The availability of N and P in the soil should have the opposite effect on glomalin concentrations, since plants should direct photosynthate away from AM fungi under high soil fertility (Singh 2012). It is crucial that we develop a better understanding of the direct impact of glomalin in C and N storage, so that these speculations can be ascertained.

Conclusion

Soil structure stability is strongly influenced by the nature and content of soil organic matter. Land use and management practices influencing soil organic matter will be determinants in soil aggregation. Root and fungal hyphae are among the most important biotic factors, if not the most important agents in soil aggregate stabilization. It should be clear from the arguments presented above that the rhizosphere is an extremely complex environment, the characteristics of which can be expected to vary dramatically with spatial location at an individual root, field, regional, or global level. AMF play important roles in agroecosystems, including the involvement of the extraradical mycelium in providing soil aggregation. GRSP has been shown to be correlated with soil aggregate water stability, although the mechanisms underlying this pattern are not yet understood. Phenomenological field studies, as well as incipient, more mechanistic investigations, have demonstrated that GRSP pools are susceptible to management practices and a variety of other influences at the ecosystem scale. Hence, increased understanding of the factors controlling GRSP production such as the ones reviewed here (fungal community composition, fungal physiology, and cell biology aspects) as well as others (e.g., other soil biota, soil physicochemical characteristics, and fungus–host plant species combinations) may ultimately inform management strategies aimed at maximizing soil aggregation in crop production systems or in other applications, such as restoration of disturbed lands.

Conflict of interest All the authors are declare that we have no conflict of interest in this review.

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