Glomalin: A Key Indicator for Soil Carbon Stabilization

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Abstract

In the last decades, many studies were addressed focusing on soil protection that helps sequestration and stabilization of organic carbon in soil aggregates. Soil aggregates are an association of primary soil particles, bacteria, fungi, plant root

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and soil organic matter. Plant root provides a carbon source for arbuscular mycorrhizal fungi (AMF) present in soil aggregates. AMF produces a glycoprotein glomalin which is hydrophobic, insoluble, and recalcitrant in nature. Glomalin plays a vital role in the stabilization of soil aggregates. Greater stability of soil aggregates leads to a larger amount of protected organic carbon in the soil. Thus, glomalin-related soil protein can be considered as a potential contributor in the stabilization of soil organic carbon. In the present chapter, the different aspects of glomalin composition, production, role in soil, recalcitrant nature, potential role in soil carbon locking up and stabilization are summarized and discussed.

Keywords

Glomalin · Arbuscular mycorrhizal fungi (AMF) · Carbon · Heavy metal · Biotic stress

Abbreviations

AMF	Arbuscular Mycorrhizal Fungi
BRSP	Bradford Reactive Soil Protein
GRSP	Glomalin-Related Soil Protein
HSP60	Heat Shock Protein 60
OM	Organic Matter
SOC	Soil Organic Carbon
SOM	Soil Organic Matter

1 Introduction

In the last 20 years, soil protection research has been focused on frequently discussed issues such as soil erosion, structural deterioration, potentially toxic elements, loss of biological diversity and depletion of SOM. These adverse factors directly lead to soil degradation and reduced fertility and impaired non-production function. The amount of organic matter or some of its fractions is an essential indicator of soil quality and health. Several positive effects of glomalin on soil have been demonstrated since its discovery in late 1990. In particular, they include the improvement of soil aggregation and structure stabilization, increased wind and water erosion resistance (Wuest et al. 2005), improved water regime, suppressing toxicity of pollutants (Vodnik et al. 2008), sequestration and stabilization of carbon (Nie et al. 2007), resistance to stress conditions (Hammer and Rillig 2011; Latef et al. 2016) and subsequent promotion of plant growth (Adesemoye et al. 2008). SOM affects AMF diversity and richness. Glomalin protein plays a crucial role in the stabilization of soil aggregates and their effect on SOC stabilization (Wilson et al. 2009).

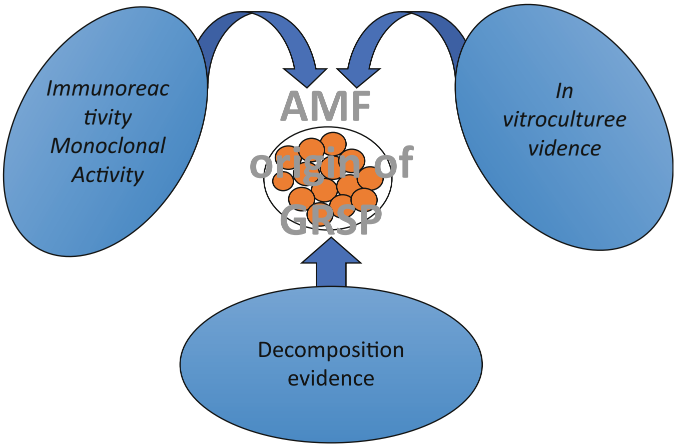


Fig. 1 Evidence suggesting the production of glomalin-related soil proteins by arbuscular mycorrhizal fungi. (Adopted from Singh et al. 2012)

Glomalin has been discovered and described by Sara Wright in 1996 during her research on vesicular-AMF. The substance was determined as a glycoprotein produced especially by arbuscular mycorrhizal-hyphae and to a limited extent also by spores. It was relatively late discovered, due to its specific properties: hydrophobicity, thermostability, and recalcitrance (Johnson and Gehring 2007; Sousa et al. 2012b). In the experimental study, glomalin was detected only in samples where roots were colonized with AMF (Smith and Read 2008b).

Figure 1 displays lines of evidence leading to the AMF origin of GRSP. Firstly, glomalin detection is proposed by methods using a monoclonal antibody which is specific to fungi (Thornton and Gilligan 1999). Secondly, decomposition tests prove that when AMF is eliminated, significant glomalin decline can be detected (Steinberg and Rillig 2003). Thirdly, the monoclonal body is used for the detection of easily extractable and immunoreactive GRSP. It reacts only with AMF members eliminating cross-reaction with other fungal species. MAb32B11 monoclonal antibody also provides the detection of spores and hyphae (Wright et al. 1996).

GRSP concentration in the soil varies depending on sites, which was linked mainly to pH variations (Wang et al. 2014). It has also been found that glomalin is primarily stored in the topsoil, and its content is lower in deeper soil layers (Wang et al. 2017). No glomalin was determined deeper than 140 cm. Further, it was detected even in rivers (Franzluebbers et al. 2000; Harner et al. 2004; Rillig et al. 2001a; Staddon 2005; Wang et al. 2018). Sites more abundant with AMF host plants or containing more carbon available for fungi are frequently detected with higher glomalin content (Treseder and Turner 2007). Seasonal variation in glomalin concentration is negligible (Steinberg and Rillig 2003). A typical concentration is 2–15 $mg.g^{-1}$ of soil. However, it is determined by the soil age and moisture content.

Table 1 GRSP content in different environments (modified) (Vlček and Pohanka 2020)

Environment	GRSP (mg.g^{-1})	References
Agricultural land	0.3–0.7	Wright and Anderson (2000) and Wuest et al. (2005)
Boreal forest	1.1	Treseder et al. (2004)
Desert	0.003–0.13	Rillig et al. (2003a) and Treseder and Turner (2007)
Temperate forest	0.60–5.8	Nichols and Wright (2005), Steinberg and Rillig (2003) and Treseder and Turner (2007)
Temperate grassland	0.23–2.5	Batten et al. (2005), Lutgen et al. (2003) and Nichols and Wright (2005)
Tropical rainforest	2.6–13.5	Lovelock et al. (2004) and Treseder and Turner (2007)
Antarctic region	0.007–0.15	Pohanka and Vlcek (2018)

There are cases of higher concentrations measured, e.g. Hawaiian soil samples (more than 100 mg. g^{-1} of soil) while lower glomalin concentration was found in soils of arid regions, less than 1 mg.g^{-1} of soil (Bird et al. 2002; Rillig et al. 2001b; Wright et al. 1998). The presence of glomalin at different sites was summarized by (Vlček and Pohanka 2020) (Table 1).

Quality and quantity of SOM strongly correlate with glomalin (Šarapatka et al. 2019). Therefore, glomalin indicates changes in soil, its degradation or erosion. Glomalin is proposed to be a suitable index of soil fertility, especially in arid soil. It was found that BRSP content positively correlates with the incidence of SOC, soil enzymes, nitrogen and phosphorus (Bai et al. 2009). Moreover, the same authors found that BRSP was a little higher in arable compared to the desert land. Despite lower BRSP content in a desert, the ratio of BRSP to SOC was much higher there, suggesting it could be an indicative level of fertility, especially in a desert. The ratio of glomalin to the total organic matter could be even used also as an indicator of soil degradation (Sharifi et al. 2018; Meena et al. 2020). Glomalin contributes to organic carbon stock and is significantly correlated to nitrogen in all soil types (Wilson et al. 2009). Land-use changes have a significant impact on the content of glomalin in soil. It was found that its content is much lower in agriculturally used land compared to native or afforested land (Rillig et al. 2003b). Thus, the authors suggest that it offers a possibility of glomalin content to become a useful sensitive indicator of land-use changes.

The present chapter targets its interest to a fraction of the SOM – a protein referred to as glomalin and summarized and discussed different aspects of glomalin and its composition, production, role in soil, recalcitrant nature, potential role in soil carbon sequestration and stabilization.

2 Determination and Terminology of Glomalin

The term "glomalin" can be used only to a protein encoded by the putative gene of AMF (Rillig 2004b). The chemical structure of glomalin remains still elusive and is only operationally and vaguely defined as a product of extraction procedure. Therefore, the term "glomalin-related soil protein" is used because the isolation of specific protein glomalin has not been carried out yet. The glomalin association with other soil proteins is well characterized by (Zbiral et al. 2017). Extraction is always burdened with non-glomalin impurities; thus, GRSP has been proposed to define the correlation of glomalin content (Rillig 2004a).

Humic acids and GRSP have similar extraction procedure; therefore, these substances are co-extracted (Schindler et al. 2007). There is a study (Gillespie et al. 2011) employing sensitive methods to characterize the chemical bonds (X-ray absorption near edge structure spectroscopy, pyrolysis-field ionization mass spectrometry). The proteomic study helps to differentiate GRSP mixture that contains humic acids, proteins of non-mycorrhizal origin and abundant heat-stable proteins related to soil and bacteria (Gillespie et al. 2011). Important substances from the view of availability, concentration or determination of glomalin are secondary metabolites, mainly tannins (Halvorson and Gonzalez 2006; Vlček and Pohanka 2020). In all the methods applied, the product is still a mixture of glomalin with co-extracted molecules, but their mutual link has not been defined yet (Schindler et al. 2007).

GRSP was first operationally determined by a monoclonal and glomalin-specific monoclonal antibody (MAb32B11) bound to a protein present in disrupted spores of *Glomus intraradices* (Wright and Upadhyaya 1996). The substances detected by the immunological method are called "immunoreactive soil protein". The outline of Glomalin Formal terminology is in Table 2 (Rillig 2004a).

Generally, all methods for total GRSP and soil proteins estimation suffer from impurities. Thus, methods are considered only as semi-quantitative (Redmile-Gordon et al. 2013). The most frequently used is the citrate method (Wright and Upadhyaya 1996) carried out under harsh conditions, including autoclaving of soil in a sodium citrate buffer at 121 °C, and followed by glomalin precipitation using trichloroacetic acid. The obtained extracts may be purified using 100 mM sodium borate solution (Schindler et al. 2007). Consequently, Bradford assay is used for its quantitative analysis (Nichols 2003; Treseder and Turner 2007). The improvement is sometimes applied to distinguish the proteinaceous materials from co-extracted humic materials using the modified Lowry microplate method (Redmile-Gordon et al. 2013). The particular substances related to glomalin are stated in Table 2.

Moreover, the GRSP can be classified as easily extractable and residual fractions (Lovelock et al. 2004). The easily extractable part is obtained at mild extraction conditions (121 °C, 30 min, 20 mM citrate, pH 7) in an autoclave, while the residual fractions at harsher extraction conditions (121 °C, 50 mM citrate, pH 8) in 1-h increments until the supernatant is colourless. The extracts are precipitated using hydrochloric acid (Schindler et al. 2007). This is beneficial mainly if the amount of C and N is measured because trichloracetic acid may bind to proteinaceous substances,

Table 2 Formal terminology for glomalin (Rillig 2004a)

Current usage	Identity	Proposal name/ usage	Justification
Total glomalin	BRSP (after autoclave/ citrate extraction)	BRSP	Bradford assay is non-specific for particular protein
Easily extractable glomalin	BRSP (easily extracted; autoclave/citrate)	EE-BSRP (easily extracted; BRSP)	Bradford assay is non-specific for particular protein
Immunoreactive glomalin	Immunoreactive (MAb32B11) soil protein (after autoclave/citrate extraction)	Immunoreactive (MAb32B11) soil protein	There is the possibility of cross-protein reactivity in soil
Immunoreactive easily extractable glomalin	Immunoreactive (MAb32B11) soil protein (easily extracted; autoclave/ citrate)	Easily extracted immunoreactive (MAb32B11) soil protein	There is the possibility of cross-protein reactivity in soil
Glomalin	Immunoreactive (MAb32B11) soil protein (easily extracted; autoclave/ citrate extraction)	GRSP	"Glomalin" in the currently used sense refers to very different entities

and thus it gives inaccurate C contents (Wright and Upadhyaya 1996). Easily extractable GRSP is believed to be produced newly or to be a recently decomposed fraction of GRSP while the total GRSP is considered to be an aged and more stable fraction of GRSP (Wright and Upadhyaya 1996).

The near-infrared spectroscopy detection method can be applied to replace the laborious high-pressure extraction of GRSP (Zbiral et al. 2017). The results showed fast GRSP determination during the simultaneous determination of other parameters such as oxidizable carbon, total carbon and nitrogen. Near-infrared spectroscopy GRSP determination method has also been successfully used in work by Heinze et al. (2013).

3 Composition

Glomalin is a protein that is very difficult to be extracted. It is often indicated as BRSP or GRSP containing some other additional proteins (Nichols 2003; Rillig et al. 2001b; Treseder and Turner 2007) and phenolic substances, such as tannins. The impurities represent up to 40% of plant litter and maybe a part of many biochemical processes in the soil (Appel 1993; Fierer et al. 2001; Hättenschwiler and Vitousek 2000; Kraus et al. 2003). Glomalin extracted from the soil contains 28–45% C, 0.9–7.3% N, and 0.03–0.1% P (Sousa et al. 2012b; Wang et al. 2017). Glomalin may also encompass metal ions depending on soil type (Huang et al. 2011; Gadkar and Rillig 2006). It may cover nearly a third of the soil carbon level and 1–9% of bound iron (Nichols and Wright 2005) which is responsible for the red colour of glomalin extract (Wright et al. 1998). Elemental analysis results combined with infrared and nuclear magnetic resonance spectroscopy data of GRSP revealed a high content of aromatic (42–49%) and carboxyl groups (24–30%), carbohydrate (4–16%) and low aliphatic substances (4–11%), which is not typical for glycoproteins but is closer to the molecular feature of humic acids (Schindler et al. 2007).

Glomalin was discovered to possess three N-glycosylation sites in its structure (Gadkar and Rillig 2006). Its structure seems to be a complex of N-oligosaccharides (Wright et al. 1998). There are even aliphatic amino acids with methyl, methylene and methines groups, polymeric with metal ions with methine being part of the peptide backbone (N–CH–C=O) (Rillig et al. 2001b). Metal ions are joined to auto-fluorescent compounds. It was reported that GRSP comprised of 49 fluorescent substances, seven functional groups, and some other elements (Wang et al. 2015b). The same study emphasizes that the composition and characterization of GRSP are more complicated than it was thought formerly. However, its biochemical structure has not been fully revealed yet (Gao et al. 2019).

Another knowledge gap on glomalin structure is whether it is a substance of consistent composition. There is a theory suggesting that glomalin composition is variable with quite substantial differences depending on sites of glomalin occurrence (Wang et al. 2014). The hypothesis is encouraged by the study assessing GRSP content difference on farmland and 30-years afforested farmland (Wang et al. 2015a). It highlights that the soil properties were significantly affected not only by the difference in GRSP concentration but also by its variable composition. There is another interesting hypothesis of Magdoff and Weil (2004) based on different organic carbon concentration in glomalin (27.9–43.1%). They stated glomalin could not be a product of an expressed gene but rather a mixture of organic matter with parts reactive to immune probes.

4 Glomalin Pathways

GRSP production is under the control of hyphae (Rillig and Steinberg 2002; Singh et al. 2012). Gadkar and Rillig (2006) reported that cell walls of hyphae contain the most considerable amount of glomalin and spores rather than secreted out of cell walls (Driver et al. 2005; Wright and Upadhyaya 1996). Results indicate that a primary function of glomalin is in fungal hyphae, and its other impact to the soil is secondary (Purin and Rillig 2007). It has been confirmed by a study examining different physical condition on hyphae growth. The glomalin primary function in hyphae comprises tolerance to grazing stress (Hammer and Rillig 2011), enhanced soil aggregate stability as hyphae grow better in aggregated soil (Rillig and Steinberg 2002) or toxicity protection (Ferrol et al. 2009; Lenoir et al. 2016). Based on this system, the presence of glomalin has been confirmed together with the putative gene for glomalin in proliferating mycelia (Gadkar and Rillig 2006; Purin and Rillig 2007). Even though glomalin is an AMF metabolite produced by hyphae, its concentration is not correlated to their length (Lutgen et al. 2003; Treseder and Turner 2007).

Glomalin is a homologue of HSP60, which was suggested based on a high identity of the amino acid sequence (Gadkar and Rillig 2006). HSP60 is a product of prokaryotic or eukaryotic cells in conditions of environmental stress (Chen et al. 2015). The glomalin encoding gene was indicated as GiHsp 60 and was isolated *in vitro* from *Glomus intraradices* (Gadkar and Rillig 2006). Thus, the discovered homology suggested that the original function of glomalin might be the protection of fungi (Lenoir et al. 2016).

The way how the glomalin is stored in the soil is unknown. There are two possible pathways. The first one assumes glomalin is a permanent part of the AMF and is released into the soil after hyphae disintegration. In such a case, it is an essential functional component of AMF (fungal tissue) with negligible impact on soil (Driver et al. 2005). The second less possible route is the secretion of glomalin as a metabolite by AMF hyphae. The latter would indicate certain mobility of glomalin within the soil. However, it could have been more readily decomposed by the soil microflora (St-Arnaud et al. 1996). Nevertheless, it was measured that 80% of glomalin is located in hyphae (Driver et al. 2005). However, a complex structure of soil suggests there might be some other factors or linkages entering the glomalin-soil relationship (Rillig 2004a).

5 Arbuscular Mycorrhizal Fungi

Soil microorganisms associated with plant roots are referred to as AMF. They are creating symbiotic relation, which is beneficial for both fungi and plants. This association of a plant and microorganism represents the most widespread type of symbiosis (Smith and Read 2008b). AMF group belongs to the phylum *Glomeromycota* (Schussler et al. 2001), which is also the most significant group of fungi producing high amounts of glomalin, compared to other groups (Wright and Upadhyaya 1996). Phylogenetic analysis revealed common ancestors for Ascomycota and Basidiomycota with AMF. Some fossils records of *Glomeromycota arbuscula* suggest that AMF played an essential role in forming terrestrial ecosystems already 250–400 million years ago (Harper et al. 2013; Redecker 2000; Remy et al. 1994; Schussler et al. 2001). These records suggest that *Glomeromycota* were participating in the colonization of terrestrial ecosystems by plants in its earliest stages, which supports the theory that they assist in the process (Blackwell 2000; Pirozynski and Malloch 1975; Simon et al. 1993).

Taxonomy of *Glomeromycota* is relatively young. Before 1974, the majority of AMF was classified in the genus *Endogone*. Since then (Trappe and Gerdemann 1979), AMF has been classified into four different genera: *Glomus*, *Sclerocystis*, *Acaulospora*, and *Gigaspora*. The recent taxonomy classification in detail was published by (Young 2012). Taxonomical classification of *Glomeromycota* is visualized in Fig. 2.

Phylum *Glomeromycota* currently includes about 220 described species (Blaszkowski et al. 2012). Lee et al. (2013) reported that there are more than 240 species, and their genetic and functional diversity is much richer than the

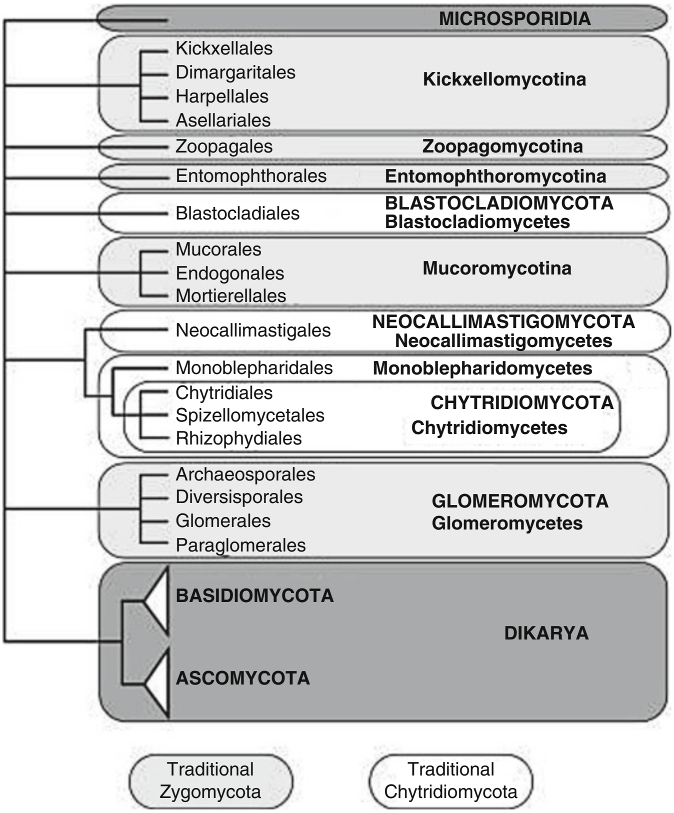


Fig. 2 Taxonomy of fungi. Branch lengths are not proportional to genetic distances. (Adopted from Hibbett et al. 2007)

morphological diversity. Most of them were defined by the morphology of the spore, which has turned it out to be a wrong way of classification (Morton and Redecker 2001; Redecker 2000). Morphology of spores is insufficient to assess the diversity of fungi as their genome is highly diverse. There are differences even within a species as they can vary in the effect on a symbiotic plant. Functional diversity might be probably resulting from a combination of plant and AMF (Lee et al. 2013). Recently, DNA sequencing was used to reduce the number of taxa.

Arbuscular mycorrhiza can be found in 70–90% (Blaszkowski et al. 2012) or 80% (Fitter et al. 2000; Smith and Read 2008a) of vascular plants (i.e. most of *Embryophyte* species). AMF has adapted symbionts of more than 200,000 plant species (Lee et al. 2013). AMF has a very low host specificity (Smith and Read 2008b). The mixtures of AMF very often colonized a single plant (Helgason et al. 1999), but the combinations of plant-fungus symbionts are known to be more or less favourable.

Crops which are highly dependent on AMF are, for example, corn (*Zea mays* L.) and flax (*Linum usitatissimum* L.). Mycorrhiza is advantageous for wheat (*Triticum* spp.), barley (*Hordeum* spp.), oats (*Avena sativa* L.), legumes (*Leguminosae*) or potato (*Solanum tuberosum* L.) but they do not show dependency on it. There are also few plants, which do not form a symbiosis with the AMF at all: among them are families *Brassicaceae*, *Amaranthaceae, Polygonaceae,* and the better-known crops mustard (*Brassica juncea* L.), rape (*Brassica napus* L.), sugar beet (*Beta vulgaris* L.), spinach (*Spinacia oleracea* L.), and buckwheat (*Fagopyrum esculentum* Moench) (Harley and Smith 1983; Plenchette et al. 1983; Thingstrup et al. 1999).

Generally, *Leguminosae* plants are capable of binding air nitrogen. Thus they can saturate their own N need and even supplement soil with N (Mikanová and Šimon 2013). This is crucial for agricultural productivity as non-*Leguminosae* are supplemented with nitrogen via *Leguminosae* (Stern 1993), especially when growing mixed culture, i.e. *Leguminosae* and non-*Leguminosae* at the same land. The transfer of nitrogen from nitrogen binding plants is indicated as rhizodeposition (Fustec et al. 2010). It has been found out that transfer between the plant species provided by mycorrhizal bridges joining roots of plants grown in mixed culture (Bethlenfalvay et al. 1991; Laberge et al. 2010; Meng et al. 2015; Walder et al. 2012; Meena et al. 2018).

Arbuscular mycorrhiza is essential for the proper functions of the majority of terrestrial ecosystems, e.g. boreal forests or heath (Read 1991). Differential advantage in succession within the ecosystem is provided by AMF (van der Heijden et al. 1998). Arbuscular mycorrhiza is endomycorrhiza, i.e. the root cells of vascular plants are penetrated with the fungus (see Fig. 3). Inside the root cells, a pouch (vesicle)-shaped storage organs are built. Moreover, a tree-like structure (arbusculus) is formed beyond the root when the fungus invades the roots (Fig. 4). The highly specialized symbiosis or mutualism was formerly known as "vesicle-arbuscular mycorrhiza". The mutualistic relationship enables AMF to enrich plants with minerals and elements from the soil (mainly phosphorus), and the plant provides organic substances from the photosynthesis.

As can be seen in Fig. 3, upon ectomycorrhizae (green) plant root cells are not penetrated by the fungal hyphae, but a covering mantle of fungal tissue around the root is created. In contrast, endomycorrhizal fungi (yellow) penetrate cortical cells and create arbuscules and vesicles. At ectoendomycorrhiza, both the covering mantle and cell penetration may occur.

The root surface is due to the hyphae increased by up to 80% (Millner and Wright 2002). Hence, it gives the plant an access to distant nutrients and elements that are hardly mobile in the soil. Nutrients are also more bio-available, e.g. phosphorus. AMF assists in litter decay and transports already released nutrients to the plant (Nuccio et al. 2013). The ways how nutrients can be easily reached are shortening distances, increasing solubility and affinity of P ions and increasing the area of its absorption (Bolan 1991). In addition to a direct positive effect on plant growth, arbuscular mycorrhiza benefits the plant habitat indirectly by improving the soil properties, in particular the ability to enhance the stability of soil aggregates (Bayer et al. 2001). AMF itself presents 5–50% of microbial soil biomass and significantly

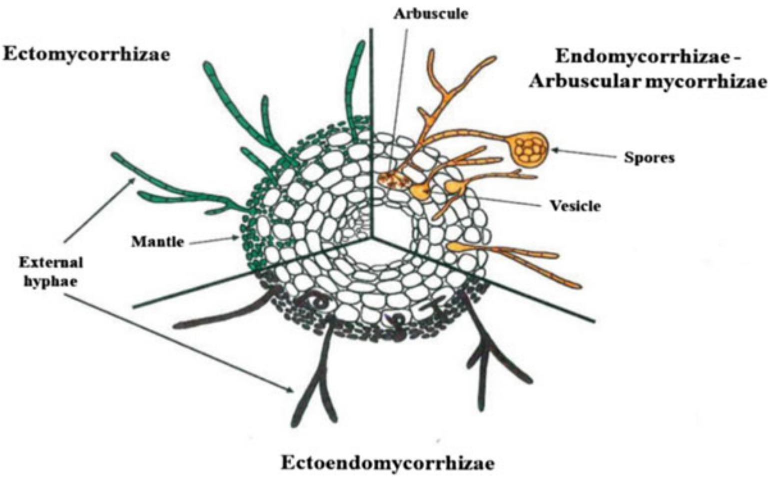


Fig. 3 Three different types of symbiotic associations between a mycorrhizal fungus and plant roots. (Adopted from Ganugi et al. 2019)

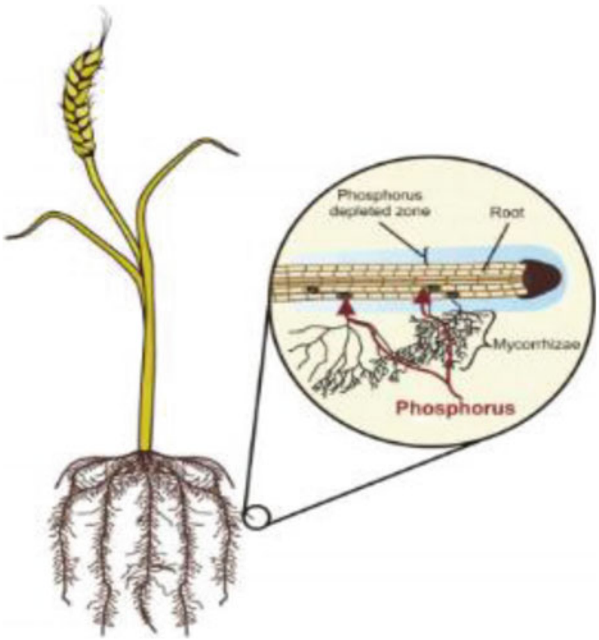


Fig. 4 Arbusculus structure expanding plant root surface. (Adopted from Bolduc and Hijri 2011)

contributes to organic matter content in the soil. AMF spore density was found to have a strong relationship to SOC, BRSP, and activity of soil acid phosphatase (Bai et al. 2009). Even the soil polluted by heavy metals shows a strong correlation of present AMF to GRSP, SOC and organic matter (Yang et al. 2017).

AMF is related to soil enzymes which are significant for the processes of organic matter mineralization (Zhou 1987). Soil enzyme activity may indicate microbial activity which is crucial for soil health and quality (Tarafdar and Marschner 1994). It was evidenced by a strong relationship of BRSP and soil enzymes, such as acid phosphatase and urease (Bai et al. 2009). Soil enzyme activity was found to be significantly increased by AMF inoculation, such as dehydrogenase, urease, saccharase, phosphatase by 6–225% (Qian et al. 2012). The fact is also confirmed by the study of (Wu et al. 2014b) who stated mycorrhiza significantly enhanced activities of β-glucosidase, peroxidase, phosphatase, and catalase, but suppressed the activity of polyphenol oxidase. The activity of hydrolytic enzymes is significantly related to glomalin, SOM, and soil structure (Gispert et al. 2013). It is interesting GRSP produced by AMF, and relevant soil enzymes are not dependent on external P content (Barto et al. 2010; Wang et al. 2015b). Soil enzyme activity was tested in the experiment using AMF inoculated plants under drought stress. Inoculated plants showed higher activity of peroxidase and catalase in both cases, with or without induced drought stress. The activity of polyphenol oxidase was affected neither by inoculation nor drought stress (Wu et al. 2008).

6 Role of Glomalin in Soil

Glomalin is not beneficial solely for fungi, but also for other soil organisms. It suggests the dual functionality of glomalin: physiological in the AMF mycelium and secondary in soil habitat (Purin and Rillig 2007).

6.1 Soil Aggregation and Carbon Storage

Soil resistant to water and wind erosion must be aggregated, stable, and with infiltration suitable for microorganisms and other organisms' growth (Bronick and Lal 2005). The soil fertility is based on its aggregation via: retaining nutrients near plant roots; sustained porosity enabling infiltration of water and air; carbon stock, protecting from carbonaceous compound decomposition; and diminishing erosion impact (Nichols and Wright 2004a). Well aggregated soil also prevents wind and water erosion as micro-aggregates are bound to macro-aggregates and thus cannot be easily washed by water or taken by the wind.

The factors affecting soil aggregation were analysed (Rillig and Steinberg 2002) and reported on the direct contribution of root length and glomalin to water-stable aggregates. Many authors pointed to the linkage between arbuscular mycorrhiza and stability of soil aggregates operating via glomalin (Rosier et al. 2006; Meena and Lal 2018; Wright et al. 1996) which is beneficial for AMF and host plant. Interestingly, glomalin effect was found to pose a much stronger effect compared to AMF hyphae. The many authors suggested that glomalin is significantly contributing to the stabilization of soil aggregates. Aggregate water stability and GRSP content in the environment strongly correlate (Bedini et al. 2009; Rillig 2004b; Rillig et al. 2010;

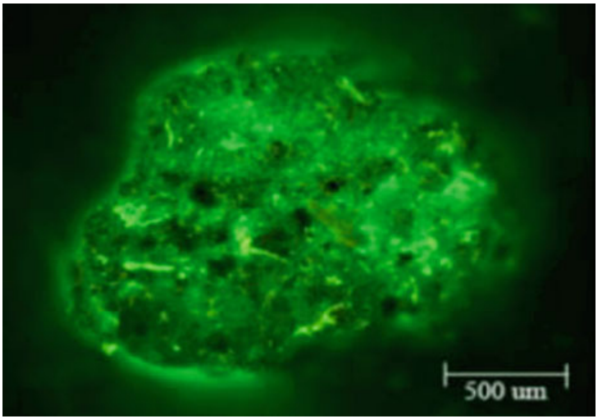


Fig. 5 Fluorescent visualization of glomalin in soil aggregate. (Adopted from Nichols et al. 2013)

Wright et al. 1998; Wu et al. 2014a; Driver et al. 2005) across broad spectra of soil types (Wright et al. 1998) and even in soil polluted by heavy metals (Yang et al. 2017). This might be the reason for GRSP persistence in soil (Gillespie et al. 2011).

Glomalin-related protein works as sticky glue joining soil particles together (Rillig and Mummey 2006). There is evidence that glomalin production is higher in non-aggregated to aggregated soil. Because hyphae of AMF grow better in aggregated soil, glomalin production is enhanced in site with impaired aggregate properties. It seems glomalin controls sub-optimal conditions for hyphae growth by aggregating soil particles into larger lumps (Rillig and Steinberg 2002). Polysaccharides of glomalin are sticky and keep smaller aggregates together. Iron creates bridges binding clay minerals and aliphatic amino acids. The complexes of organic (glomalin or humin) and mineral substances (clay) form a hydrophobic layer which protects soil from erosion by water and wind (Nichols and Wright 2004a). Structure of glomalin-bounded aggregate can be seen in Fig. 5 using fluorescent visualization of glomalin.

AMF and their exudates (including GRSP) can decrease the permeability of soil surface by increasing its hydrophobicity which stabilizes soil aggregates. The theory of aggregation ability may be supported by the discovered homology with HSP60 (Gadkar and Rillig 2006) as it plays the primary role in cell adherence (Hennequin et al. 2001). Aggregation is also a result of hyphae mediating stability (Tisdall et al. 1997). Their structure resembles “a flexible string bag” releasing GRSP and showing plasticity (Graf and Frei 2013). Aggregate stability is also promoted by fine plant roots (Tisdall and Oades 1979). Expanded system of roots provides more chances for AMF colonization, thus greater hyphae growth and more GRSP exudates affecting aggregate stability (Kohler-Milleret et al. 2013). The aggregate stability may also be enhanced by substances called hydrophobins which are released by AMF (Rillig and Mummey 2006).

Nevertheless, it is necessary to note that the correlation between soil aggregates stability and glomalin content is curvilinear. It means there is a point of saturation of no further increase in water aggregate stability (Rillig 2004b). The phenomena may be caused by the fact that all pores are already filled with glomalin. Aggregation stability is caused even by recalcitrance and long-term turnover of glomalin (Varma and Podila 2013).

However, some studies doubt whether aggregate stability is affected by glomalin (Purin and Rillig 2007). There was investigated a negative correlation between soil aggregation and AMF-mediated glomalin as the main cause of the soil aggregate stability (Rillig et al. 2003b). The stability was motivated mainly by carbonate concretions in Mediterranean steppes. Treated pine forestland with nitrogen addition within two years, causing an increase in GRSP and SOC did not affect aggregate stability (Sun et al. 2018). The authors assumed that aggregate stability formation is a long-termed process and depends on binding agents. Nevertheless, all the studies are based on macro-aggregates, and there is nothing known on micro-aggregates and related effects of glomalin. Furthermore, the contribution of some other factors, such as other microorganisms, could be involved in aggregates stabilization increase. Finally, glomalin is only a part of an organic substances pool. Thus it is complicated to predict their relation to the glomalin effect on aggregation (Varma and Podila 2013).

6.2 Resistance to Abiotic Stress

AMF reacts to abiotic stress differently. Their diversity and abundance are usually higher at non-disturbed sites. Polluted or sites with various abiotic stress are characteristic for lower AMF species richness with the prevalence of *Glomeraceae*. Even though AMF are sensitive to abiotic stress, some species have developed several mechanisms to defend against various stresses. The mechanisms involve antioxidant system, membrane lipid transformation or, e.g. sequestration processed by glomalin (Lenoir et al. 2016). AMF and GRSP can also improve the properties of soil and plants under various stresses, e.g. drought (Chi et al. 2018; Zou et al. 2013), salinity (Nichols 2008; Ibrahim 2010), extreme temperatures, nutrient deficiency, heavy metals (Li et al. 2015), organic compounds contaminations (Joner and Leyval 2001), and others (Gao et al. 2019).

6.2.1 Water Stress

The contribution of glomalin to reduce water loss is unknown as the results of the studies are inconsistent. Glomalin may cause reduced evaporation of water during drought (Gao et al. 2019) as it creates a polymeric hydrophobic surface of soil aggregates avoiding water loss (Nichols 2008) which might be related to the ability of glomalin to decrease the natural decomposition of water-soluble soil aggregates (Scott 1998; Thomas et al. 1993). AMF affected water retention positively through the glomalin effect in the study of Wu et al. (2008). On the other hand, investigated water repellence was not correlated to the glomalin presence, suggesting hydrophobicity is rather caused by AMF hyphae forming string-bag like structure holding particles together (Miller and Jastrow 2000). BRSP concentration was weakly increased by drought stress without significant differences (Wu et al.

2008). However, soil water deficiency-induced total GRSP and easily extractable GRSP production together with a water-stable aggregate of a size larger than 0.25 mm (Zou et al. 2014). Soil water repellence is probably a result of more factors and more hydrophobic substances released by plants, roots, and microorganisms (Hallett et al. 2003). Such a mixture of soil hydrophobic substances can behave differently at various moisture conditions (Dekker et al. 2001). When soil is wet, hydrophilic parts of the substances are not bound, and such soil is strongly hydrophilic. In case of moisture drop to some level, hydrophilic groups bond tightly together, exposing the hydrophobic part of the substance covering soil aggregates. It leads to the enhancement of water repellence (Dekker et al. 2001; Hallett et al. 2003). The effect is known as dual surface hydrophobicity (Morales et al. 2010), see Fig. 6.

6.2.2 Pollution by Heavy Metals

The AMF symbiosis brings benefit to plants, even in the polluted environment containing heavy metals. Fungi hyphae can accumulate the toxic elements in their cells to protect the roots of a host plant (Gonzalez-Chavez et al. 2002). GRSP is a factor affecting toxic elements in soil (Gao et al. 2019), e.g. by buffering and binding capacity (Wang et al. 2019), ability to stabilize or reduce the availability of toxic metals for host plants or microorganisms (Rillig 2004b). The topics are discussed more in detail in the following text devoted to soil remediation.

6.2.3 High Temperature

Despite the fact glomalin is tolerant to high temperature, unlike other proteins, the study applying different very high laboratory temperatures on different soil characteristics done (Lozano et al. 2016) discovered glomalin to be sensitive to fire. Therefore, the authors suggested that glomalin is a suitable indicator of fire severity. The findings are reported by other authors (Sharifi et al. 2018; Wuest et al. 2005). However, the correlation between fire and the glomalin concentration was not found (Knorr et al. 2003).

6.3 Biotic Stress

The hyphae protect plants against pathogens. It has been found that fungi and the plants have a system for communication. In the presence of a pathogen, the plant is warned early by the fungus and can release root exudates stimulating the growth of antagonistic microorganisms to the pathogens (Borowicz 2001). Glomalin has possibly originated as a coating of hyphae protecting from water and nutrients loss before they reach the roots of the host plants and as a protection from adverse microorganisms (Nichols 2008). However, there are theories linking glomalin production to AMF grazing stress caused by another soil biota. Glomalin production could be triggered by suboptimal conditions of mycelium growth in *Glomus intraradices* (Hammer and Rillig 2011). The experiment used fungus, which can clip AMF hyphae. The stress-induced by clipping has motivated AMF to increase

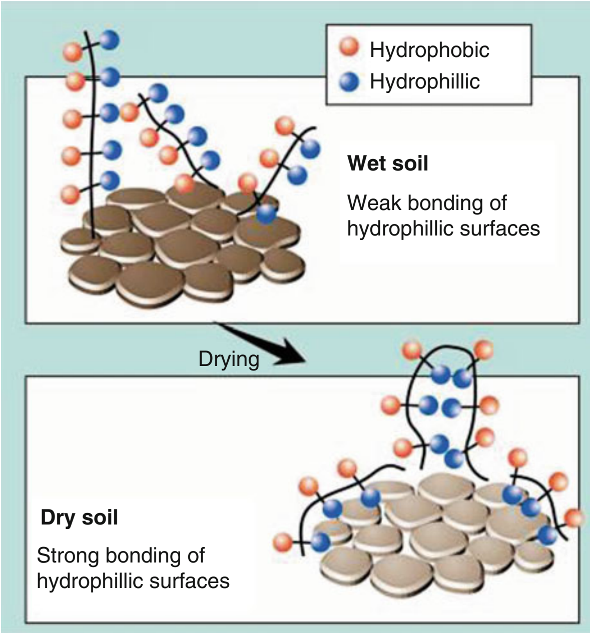


Fig. 6 Dual surface hydrophobicity of substances bound to soil particles. (Adopted from Hallett 2007)

glomalin production. This suggests glomalin is involved in defence from the grazing stress.

The study of Purin and Rillig (2007) hypothesized that glomalin might reduce the palatability of AMF in comparison to other soil fungi for microarthropods based on the study of Klironomos and Kendrick (1996) who also have confirmed that narrower hyphae further from plant roots are preferred for grazing. This theory supports the hypothesis of stress/inducible glomalin production and consensus with findings of another study (Driver et al. 2005) which found 80% of glomalin stock in hyphae and by the high degree of HSP60 and glomalin homology (Gadkar and Rillig 2006).

6.4 Glomalin Turnover and Recalcitrance

Chemically, it is clear that glomalin belongs to a group of glycoproteins produced by hyphae and AMF spores. The results suggested that it is hydrophobic, thermally stable and recalcitrant, which may be the reason for its relatively late discovery (Sousa et al. 2012a). The extent of recalcitrance ability is given by the recalcitrance index, which is determined by a ratio of alkyl and aromatic C to O-alkyl, carbonyl and carboxyl C (Ostertag et al. 2008). Zhang et al. (2017) investigated the recalcitrance index in the forest in a stage of natural succession (from 20–145%).

Based on C_{14} analysis, (Rillig et al. 2001a) estimated the average turnover time of glomalin for 6–42 years in the environment. Miller and Kling (2000), on the other hand, estimated the range to only 2.6–3.8 years. One possible explanation for this disparity may be that the AMF settles two functionally distinct sites: roots and soil. It is also one of the possible reasons for problematic assessment of AMF flows or time of environmental persistence as recognized by different authors (Miller and Kling 2000; Staddon 2003; Steinberg and Rillig 2003; Zhu and Miller 2003). Bonded organic carbon found in the clay fraction (organo-mineral complexes) shows a similar persistence time (Rillig et al. 2001b), which may indicate protection of glomalin from degradation by binding to clay minerals in soil (Lobe et al. 2001). Relatively slow glomalin decomposition can cause accumulation of the glomalin up to high concentration (Treseder and Turner 2007). Another interesting study (Knorr et al. 2003) found out a faster BRSP turnover in the forest compared to agricultural land. Treseder and Turner (2007) considered that soil microorganisms use a relatively high amount of N in glomalin as a source of nitrogen. Thus, the mineralization may be faster in soil with lower fertility where N is limited. The second theory is that there may be differences in glomalin chemical structure varying upon different ecosystems causing variable decomposition rate.

7 Glomalin Locking Carbon Stabilization and Sequestration

SOC pool is controlled by mechanisms of carbon sequestration and stabilization, which dramatically affects soil fertility (Goh 2004). Soil carbon can be found in two pools of SOM. One is easily degradable, indicated as particulate organic matter, and the other one is a heavy and recalcitrant fraction which is resistant to microbial decomposition, indicated as humic substances (Prasad et al. 2018).

AMF enhances carbon sequestration (Wang et al. 2009), but its production is substantially involved by the plant. The higher plant's nutrient demand leads to a higher amount of carbon supply provided by AMF. Most of the carbon is utilized to produce glomalin (Treseder and Turner 2007). The fungi may utilize up to 85% of soil carbon (Treseder and Allen 2000), Harris and Paul (1987) estimated that the rate of plant carbon transformation to the AMF can achieve 40–50% of photosynthetically assimilated carbon. Conservative estimate is 10–20% (Jakobsen et al. 2003) even in coastal marine systems (Wang et al. 2018). It was revealed that 27% of soil carbon is stored as glomalin which represents the main part of organic matter. Practically, glomalin encompasses one-third of the global carbon stock, while humic acid contributes to soil carbon by only 8%. Glomalin weight is 2–24x greater to humic acid (Wright and Nichols 2002). Glomalin is considered to be the largest pool of soil nitrogen and an essential reservoir of other elements under extractable SOM (Nichols and Wright 2004b). Glomalin concentration is responding to carbon fluxes and elevated carbon dioxide (Treseder and Turner 2007). Decomposition test with CO_2-C revealed glomalin is significantly correlated to active organic carbon stock in the soil in all the soil types and land-uses. It points to the fact that glomalin may be controlled the similar way as carbon in soil (Rillig et al. 2003b).

Soil sequesters carbon from the atmosphere, but it is accumulated only up to some level. Its potential to accumulate carbon is mainly based on the ability of carbon stabilization (Goh 2004). Carbon stabilization is tightly linked to many factors. One is soil aggregation and stability of soil aggregates. Stabilization of soil aggregates multiplies the significance of glomalin because the stabilization protects the inner part of carbonaceous substances from degradation (Wright 2000). Organic matter encapsulated in soil aggregates exerts suppressed decomposition (Prasad et al. 2018). Glomalin forms a hydrophobic layer on hyphae and keeps soil aggregates together, causing physical SOM/carbon stabilization inside (Rillig et al. 1999b). Alternatively, it is hypothesized that glomalin decelerates the natural disintegration of soil aggregates (Thomas et al. 1993).

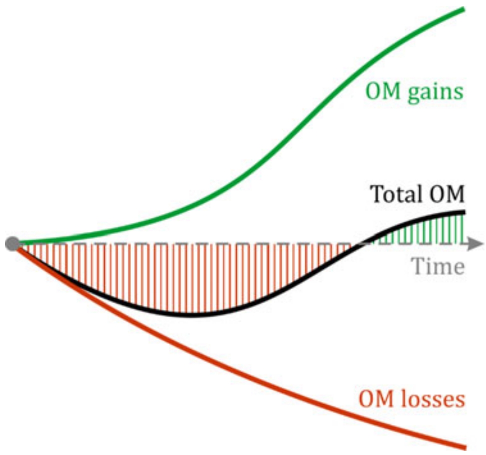
Soil carbon stock stability is enhanced even by the fact that when carbon is sequestered into glomalin, it becomes a part of the recalcitrant and hardly decomposable part of soil carbon stock. It should not be neglected that carbon in glomalin is stabilized as its turnover takes years depending on the site (Rillig et al. 2001b). Stubborn structure of glomalin-like proteins promotes sequestration of SOM, as Zhang et al. (2017) found that GRSP recalcitrance index is higher than the recalcitrance index of SOC in the environment of natural succession. In the same study, the authors suggest that GRSP contributes to SOC accumulation through retaining C and by recalcitrant composition prolonging C soil stock turnover.

Nowadays, it is not clear whether carbon contained in hyphae leads to SOC accumulation (Zhang et al. 2017). Some studies suggested AMF is conductive to SOC accumulation (Rillig 2004a; Zhu and Miller 2003), but some are claiming AMF is insignificant or even disadvantageous because results showed AMF accelerated SOM decomposition (Godbold et al. 2006; Hodge et al. 2001; Meena et al. 2020a; Tu et al. 2006). AMF may lead to SOC decomposition or even to soil carbon loss in the short term. Nevertheless, counteract was achieved by gaining C stock through a higher amount of recalcitrant compounds (Verbruggen et al. 2012), leading to long-term soil carbon stabilization. The dynamics of a short- and long-term carbonaceous compound stock can be seen in Fig. 7. However, AMF can accelerate the degradation of fresh residue, and it suppresses the degradation of former and aged SOC (Wei et al. 2019).

AMF is suggested to accelerate SOC accumulation at elevated carbon dioxide concentration (Antoninka et al. 2011; Meena et al. 2020b). It raises the question of whether AMF can buffer an increased amount of CO_2 within the global scale. The study of (Chen et al. 2012) poses a controversy attitude as their compelling short-term experiment carried out at an elevated concentration of nitrogen and CO_2 resulted in C pool loss caused by the accelerated rate of SOM decomposition. Nevertheless, the short-termed experiment could have detected a loss in C pool caused by accelerated decomposition, but in the long-term carbonaceous compound would instead increase as microorganisms and plants would be triggered by the decomposed compounds (Verbruggen et al. 2012), as explained in Fig. 7.

AMF must invest carbon to produce glomalin. Thus, higher carbon content enables AMF to produce higher glomalin stock. An elevated amount of carbon dioxide leads to the growth of glomalin concertation (Treseder and Turner 2007) and the growth of AMF in soil (Kasurinen et al. 1999). Thus, enhanced soil carbon accumulation presents a possibility to mitigate global climate change, especially

Fig. 7 Dynamic of gains and losses of organic matter. (Adopted from Verbruggen et al. 2012)



nowadays when degraded and nutrient-depleted soil could become a sink for an excessive amount of atmospheric carbon (Goh 2004).

In sandstone grassland, AMF reacted to elevated CO_2 level by increasing their hyphal length, but in serpentine grassland not (Rillig et al. 1999a). Under the same conditions, GRSP production was promoted in grassland (Rillig et al. 1999b), steppes (Rillig et al. 2003b) but not in the temperate forest (Garcia et al. 2007). The excessive content of carbon dioxide also caused glomalin gain in smaller soil aggregates (Rillig et al. 1999b). AMF reacted to the same condition in polluted soil by Pb and Cd. Sequestration of more heavy metals was detected as more GRSP was produced (Jia et al. 2016). The studies indicate there is a possibility that global change with its rising levels of CO_2 could increase soil aggregation and change soil structure, which could imply other studies of soil stabilization (Treseder and Turner 2007). Nevertheless, the effect of other inorganic substances on glomalin stock is not consistent.

8 Glomalin Management in Soil

8.1 Methods to Increase or Decrease Glomalin Level in Soils

The concentration of arbuscular mycorrhiza and hence glomalin is strongly dependent on vegetation cover and soil management (Martinez and Johnson 2010; Mirás-Avalos et al. 2011; Oehl et al. 2010). Higher glomalin concentration was detected in soils with vegetation ideally supplied with nutrients (Violi et al. 2007). Currently, many scientists are trying to increase the concentration of glomalin in the soil by inoculum of mycorrhizal fungi. *Glomus mosseae* was prosperous as an AMF inoculum in the experiment (Li et al. 2015). Importantly, the impulse that would trigger glomalin production by AMF hyphae has not been accurately elucidated yet (Rillig et al. 2001b). It is alluring that there was found a positive correlation of net primary

Table 3 Glomalin and soil aggregate stability affected by crop rotation (Wright and Anderson 2000)

Sample	Stability of 1–2 mm soil aggregates	Total glomalin (mg.g^{-1})	Immunoreactive total glomalin (mg.g^{-1})
W-F	11.6 (4.11)	2.3 (0.7)	0.57 (0.08)
W-C-M	12.6 (3.4)	2.9 (0.3)	0.56 (0.16)
W-C-M-F	12.0 (5.9)	2.5 (0.5)	0.61 (0.16)
W-C-F	11.5 (6.0)	2.4 (0.4)	0.62 (0.12)
W-S-F	7.4 (3.5)	2.3 (0.4)	0.52 (0.08)
Crested wheatgrass	59.9 (19.9)	3.0 (1.5)	1.70 (1.34)
Triticale	7.3 (3.3)	1.5 (0.3)	0.41 (0.08)

W – wheat; C – corn, M – proso millet, S – sunflower, F – fallow; mean and standard deviation are in parentheses

production and glomalin stock, but not with AMF abundance (Treseder and Turner 2007).

The studies suggested a no-tillage system is better to increase in GRSP or AMF colonization in the soil as conventional tillage mechanically disrupts a network of hyphae. The experiment comparing no-tillage to conventional tillage soil management observed positive results at the length of hyphae, GRSP content, water-stable aggregates, total mycelium and total carbon when applying a no-tillage system (Curaqueo et al. 2010; Filho et al. 2002). Soil management was reported to affect glomalin concentration (Rillig 2004b). Effect of different agriculture management on soil aggregation showed the best output within no-tillage management in topsoil layer 0–20 cm (Filho et al. 2002). Contrarily, the soil with physical disruption of soil structure, e.g. by tillage, was investigated with lower glomalin content in several studies (Borie et al. 2000; Sharifi et al. 2018; Wright and Anderson 2000; Wright et al. 1999). The relation of glomalin concentration to grazing has not yet been statistically demonstrated (Franzluebbers et al. 2000). These findings suggest that GRSP production is highly sensitive to agro-technical interventions even at their short-term application (Rillig 2004b). Generally, application of lime, mineral fertilizers or pesticides and similar approaches of the agricultural management alter the soil environment and affects soil organisms (Prasad et al. 2018).

Another parameter affecting glomalin concentrations in the soil is the crop rotation (Wright and Anderson 2000), see Table 3. Based on this, the best results were achieved with crop rotation wheat–corn–millet with the application of no-tillage soil management. On the other hand, aggregation of soil was not affected by crop rotation (Filho et al. 2002).

After the application of organic material, in particular manure, liquid manure or compost increased content of glomalin is usually observed (Curaqueo et al. 2011; Oehl et al. 2004; Valarini et al. 2009). Several doses of compost were used, and the increase in glomalin content was proportional to the dose of compost (Valarini et al. 2009). The same effect was shown even on the combination of chemical fertilizer and straw in rice cultivation (Nie et al. 2007).

8.2 Effect of GRSP Treatment on Crops

Some studies deal with the treatment using exogenous easily extractable GRSP. They seem to have a promising effect on fertility and structure of the soil, plant growth and their tolerance to stress (Gao et al. 2019). Different types of treatment using easily extractable GRSP have found a positive effect on the increase in biomass, dry weight, the activity of soil enzymes, length of roots or photosynthesis intensity (Wang et al. 2016; Wu et al. 2015; Chi et al. 2018).

Soil inoculated with two AMF species was detected with elevated SOC, total and extractable GRSP in the rhizosphere. Its impact was seen in limited fungi presence and no affection of soil bacteria (Zhang et al. 2019). The authors reported that GRSP and SOC were highly related to the limited richness of fungi species. AMF inoculation also improved plant biomass, carbohydrates, BRSP, and water-stable aggregates (Wu et al. 2008).

8.3 Potential Role of Glomalin in Soil Sustainability

With all the mentioned characteristics, AMF and their product glomalin contribute to soil sustainability. AMF may positively affect soil physical and chemical properties (Gao et al. 2019), such as improved stability of aggregates (Bedini et al. 2009; Rillig et al. 2010; Wright et al. 1998; Wu et al. 2014a), reduced water loss (Zou et al. 2013), resistance to biotic or abiotic stress (Amiri et al. 2016; Ibrahim 2010; Li et al. 2015; Nichols 2008), and the soil enrichment with SOM (Verbruggen et al. 2012). Moreover, it subsidizes plants with organic substances (Quilambo 2003; Treseder and Turner 2007) which may significantly affect crop productivity (Adesemoye et al. 2008). AMF effect is a complex system improving soil health and quality and shall not be neglected at any of the agricultural intervention.

Soil sustainability may be promoted using the system of integrated nutrient management which aims to join added and natural sources for plants efficiently to maintain yield and productivity (Gruhn et al. 2000). In such systems, AMF could play a significant role as they are capable of enriching the soil with nutrients without any other intervention. AMF has been used in the experiment of (Adesemoye et al. 2008), resulting in improved nutrient and yield properties. The experiment combining the plant growth-promoting rhizobacteria with AMF brought promising results as biofertilizers and increased uptake of N, P and K nutrients by plants.

8.4 Glomalin Remediating Polluted Soil

Glomalin can sequester potentially toxic elements, and thus it may be contributing to phytostabilization in polluted soil (González-Chávez et al. 2004; Yang et al. 2017). AMF inoculation was carried out to reclaim soil in a mine resulting in significant improvement of the soil state (Qian et al. 2012).

Glomalin is able to sequester heavy metals, in particular Cu, Pb and Zn (González-Chávez et al. 2004; Chern et al. 2007; Vodnik et al. 2008). One hundred eighty-eight mg of Pb and 4.8 mg of Cu can be adsorbed by 1 g of glomalin (Cornejo et al. 2008; Chern et al. 2007). Different results were mentioned by González-Chávez et al. (2004) who tested hyphae of *Gigaspora margarita* and found even 28 mg of Cu per gram of glomalin. In mangrove wetlands, an investigation found that GRSP immobilized and sequestered heavy metals which reduced their mobility (Wang et al. 2019). The authors reported on the fact that glomalin sequesters Cu through reversible reaction and possibly via complexes (González-Chávez et al. 2004). AMF produces excessive amounts of glomalin to affect the bioavailability of copper to eliminate its toxicity to soil biota. It suggests they provoked glomalin production, as protection from Cu-toxicity, could be a primary function of the glomalin (Ferrol et al. 2009; Lenoir et al. 2016). In addition, some authors reported even some affinity of glomalin to aluminium (Aguilera et al. 2011; Seguel et al. 2016).

However, all heavy metals do not involve AMF the same way. Pb was found to be significantly more toxic to AMF, causing a reduction in the content of SOM, SOC, and GRSP, compared to Zn (Yang et al. 2017). Despite the fact, glomalin binds Cd and Pb, the overall effect on heavy metals is affected by other factors. The experiment led by Wu et al. (2014c) showed that the amount of sequestered Cd and Pb by glomalin was negligible in comparison to the sorption capacity of SOM.

9 Conclusion and Perspective

Despite considerable blank space in the understanding of GRSP and glomalin, future work can be pointed to enlarge the knowledge on soil structure, and its quality, further applicable soil management as well as new biotechnology approaches in modern agriculture (Rillig 2004a). There are still unknowns and vague information on glomalin structure and its constituents. Optimization of glomalin extraction is needed as the current methods offer results contaminated with impurities obstructing glomalin identification, such as tannins. The exact structure of glomalin is complicated as its extraction is harsh and may eliminate heat-labile proteins. Thus, new and less laborious methods of its extraction led under more moderate conditions would help the further investigation. Another obstacle to uncovering the structure of glomalin presents the fact there is a possibility glomalin can have different compositions depending on the environment. There is even a question of glomalin structure reveal ability, as some facts point to its changeable composition.

There is still missing evidence on the primary function of glomalin as it has not been discovered. The studies provide variable suggestions. Nevertheless, they agree that glomalin production is advantageous for AMF survival. The functions encompass better soil aggregation, protection from metals toxicity, protection from fungi grazers or generally higher ability to withstand impaired living conditions.

Another topic, which offers many gaps in understanding, is soil structure and glomalin concentration under elevated carbon dioxide levels, as there is a hypothesis of glomalin ability to buffer carbon dioxide excess. There are no known mechanisms and patterns of glomalin reaction and contribution to the soil which can be expected under the predicted climate change scenario. Glomalin production and decomposition shall also be investigated as the studies could provide more knowledge on its function for AMF. It could also shed some light on the prediction of glomalin content in the ecosystems affected by climate change. Currently, enhanced soil carbon accumulation presents a possibility to mitigate greenhouse gasses as degraded soil could become a sink for an excessive amount of atmospheric carbon.

Finally, soil sustainability may be achieved by the system of integrated nutrient management which aims to join added and natural sources for plants with efficiency to maintain yield and productivity. In such manner of agriculture management, there is a vast space for new biotechnological procedures comprising AMF and GRSP.

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