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Review

Glycoproteins of arbuscular mycorrhiza for soil carbon sequestration: Review of mechanisms and controls

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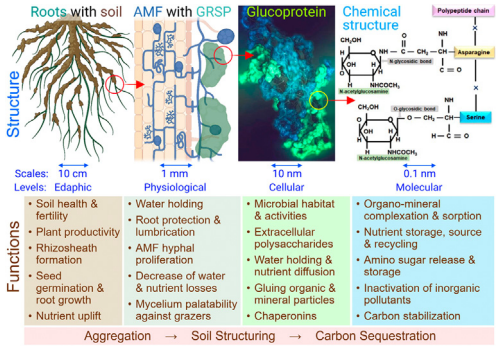
HIGHLIGHTS

- Glomalin related soil proteins (GRSP) increase C sequestration mainly indirectly.
- GRSP increase aggregate size and stability enhance AMF survival, protect hyphae.
- AMF host plants and organic fertilizers increase glycoprotein production.
- Tillage disrupts the AMF hyphal network and thus reduces GRSP production.
- GRSP are key indicators of soil quality and good agricultural management practices.

GRAPHICAL ABSTRACT



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ABSTRACT

Glycoproteins, e.g., glomalin related soil proteins (GRSP), are sticky organic substances produced by arbuscular mycorrhizal fungi (AMF). This review summarizes the information on i) the biochemical nature, physical state and origin of GRSP, ii) GRSP decomposition and residence time in soil, iii) GRSP functions, in particular the physical, chemical, and biochemical roles for soil aggregation and carbon (C) sequestration, and finally iv) how land use and agricultural management affect GRSP production and subsequently, organic C sequestration. GRSP augment soil quality by increasing water holding capacity, nutrient storage and availability, microbial and enzymatic activities, and microbial production of extracellular polysaccharides. After release into the soil, GRSP become prone to microbial decomposition due to stabilization with organic matter and sesquioxides, and thereby increasing the residence time between 6 and 42 years.
Temperate soils contain 2-15 mg GRSP g^{-1}, whereas arid and semiarid grasslands amount for 0.87-1.7 mg g^{-1}, and GRSP are lower in desert soils. GRSP content is highest in acidic soils as compared to neutral and calcareous soils. Conservation tillage, organic fertilizers and AMF inhabiting crops (e.g. maize, sorghum, soybean, and wheat) increase GRSP production and transform C into stable forms, thereby sustaining soil health and reducing CO_2

Abbreviations: AMF, Arbuscular mycorrhizal fungi; C, Carbon; GRSP, Glomalin related soil proteins; SOC, Soil organic carbon.

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emissions. Crop rotations with non-mycorrhizal species (e.g. rapeseed) and fallow soils reduce AMF growth and consequently, the GRSP production. The GRSP production increases under nutrient and water deficiency, soil warming and elevated CO_2. In the context of global climate change, increased C sequestration through GRSP induced aggregate formation and organic matter stabilization prolong the mean residence time of soil C. Protecting soils against degradation under intensive land use, stable aggregate formation, and prolonging the residence time of C calls for strategies that maximize GRSP production and functions based on reduced tillage, AMF-relevant crop rotations and organic farming.

Contents

1. Introduction

Soil organic carbon (SOC) sequestration refers to the reduction of anthropogenic CO_2 emissions by facilitating their capture and storage in biotic and soil carbon (C) pools. SOC sequestration is based on the increase of mean residence time (MRT) of C in soil (or other stable pools) to prevent its re-emission into the atmosphere (Lal, 2008; Olson et al., 2014). The keywords in this definition are: the transfer of CO_2 from atmosphere through plants into the soil, plant residues, increasing MRT, and avoiding re-emission into the atmosphere. Soil aggregation and C stabilization processes are interlinked because the water-stable aggregates protect against SOC decomposition and pave the way for C stabilization (Six et al., 2002; Totsche et al., 2018). Mycorrhizal and saprophytic fungi are the most important microbial groups for aggregate formation and stabilization, whereas bacteria are important mainly for the lower hierarchical aggregate orders such as microaggregates (Six et al., 2004).

Arbuscular mycorrhizal fungi (AMF) establish symbiotic relationships with more than 80% of terrestrial plants. AMF produce glycoprotein glomalin, more specifically glomalin related soil proteins (GRSP, often interchangeable), which are crucial for soil aggregation, C storage and soil quality improvements (Nichols, 2003; Rillig et al., 2001b; Schüßler et al., 2001). Even before the discovery of glomalin, Gupta and Germida (1988) advocated the existence of agglutinative agents (possibly microbially derived) that cemented and efficiently formed microaggregates. The mycotrophic ability of AMF (AMF colonization) and GRSP production is important to increase soil quality and protect its structure (Holátko et al., 2021). In the case of AMF-mediated soil aggregation, the indirect role of GRSP is more important than the direct role of hyphae (Rillig et al., 2002a).

To represent glomalin, a more categorical term 'Glomalin Related Soil Proteins' or 'GRSP' was proposed due to the lack of protocols for extracting pure glomalin. Subsequently, GRSP became the accepted term for glomalin (Rillig, 2004). Glomalin quantified by the Bradford protein assay is termed as 'BRSP' or 'Bradford reactive soil protein' (Table 1). The term 'glomalin' has been reserved to designate the purified product of AMF, which is measured through the monoclonal antibodies generated against AMF (Wright et al., 1998; Wright and

Table 1
Terminology, extraction and descriptions for glomalin related soil proteins (GRSP) given by various literature sources.

Extraction/Description	GRSP fraction[a,b]	Reference
Extracted from soil using 20 mM sodium citrate followed by 30-60 min of autoclaving and centrifugation	Easily extractable glomalin (EEG)	(Wright and Upadhyaya, 1996, 1998)
Extracted from soil using 50 mM sodium citrate followed by 60-90 min of autoclaving and centrifugation	Total glomalin (TG)	
Immunoreactive fraction of TG	IRTG (Immunoreactive total glomalin)	(Wright and Upadhyaya, 1998)
Immunoreactive fraction of EEG	IREEG (Immunoreactive easily extractable glomalin)	
Previously called glomalin and include both total glomalin (TG) and easily extractable glomalin (EEG) fractions	GRSP (Glomalin related soil protein)	
New terminologies for easily extractable glomalin (EEG)	EE-BRSP (Easily extractable-Bradford reactive soil protein) EE-IRSP (Easily extractable immunoreactive reactive soil protein)	(Rillig, 2004)
New terminologies for total glomalin (TG)	BRSP (Bradford reactive soil protein)/T-BRSP (Total-Bradford reactive soil protein) IRSP (Immunoreactive reactive soil protein)	
Other terms for glomalin and GRSP	DE-GRSP (difficultly-extractable glomalin-related soil protein)[c]	(Wu et al., 2014)
	Citrate extractable soil proteins (CESP)	(Holátko et al., 2021)
	Autoclaved citrate extractable protein	(Hurisso et al., 2018)
	SPRG (Soil protein related to glomalin)	(Pérez et al., 2012)
	GAHS (Glomalin associated with humic substances)	
	$GRSP_e$ and $GRSP_t$ (Easily extractable and total glomalin related soil protein)	(Liu et al., 2020)
	BRF (Bradford reactive fraction)	(Whiffen et al., 2007)
	BRS (Bradford reactive substance)	(Janos et al., 2008)
Immunoreactive fraction of TG and EEG	IRP (Immunoreactive protein)	
Extracted from root using 50 mM sodium citrate (90 min of autoclaving)	Glomalin-related root protein (GRRP) BRP (Bradford Root Protein)	(Wu et al., 2016)
Extracted from root using 20 mM sodium citrate (30 min of autoclaving)	IRP (Immunoreactive root protein)	(Rosier et al., 2008)

[a] Extracted protein may contain some thermostable compounds of plant origin, lipids, proteins, humic acid like substances and carbohydrates that survived autoclaving and could interfere with quantification.
[b] Immunoreactive fractions are quantified by Enzyme linked immunosorbent assay (ELISA) through cross-reactivity to anti glomalin antibody MAb32B11; Bradford reactive fractions by Bradford protein assay and all others by both the methods.
[c] Same soil-sub-sample is used to extract EE and T-GRSP/DE-GRSP and at some places the sum of the two fractions is known as T-GRSP.

Upadhyaya, 1996). To avoid confusion in nomenclature, this review uses AMF glycoproteins for native glomalin and GRSP for extracted glomalin (Table 1).

This review summarizes and generalizes information on the role of AMF-produced glycoproteins (GRSP) in sequestering soil C and focuses on i) the origin, biochemical nature, and physical state of GRSP in soils, ii) their decomposition and residence time, iii) the direct and indirect role of GRSP in physical, biochemical and microbial C stabilization, and iv) the impact of land use and agricultural management practices on GRSP production and its consequences for SOC sequestration.

2. An overview of AMF glycoproteins

2.1. The sources and chemical properties of GRSP

GRSP in their native form were identified as a recalcitrant, hydrophobic and sticky glycoproteins (Wright et al., 1998; Wright and Upadhyaya, 1996). The presence of N-linked oligosaccharides on AMF hyphae and carbohydrate residues (Nichols, 2003; Wright et al., 1998) corroborate the glycoproteinaceous nature of GRSP (Fig. 1). Glycosylated proteins constitute a major portion of GRSP and the specific glycan domains are responsible for the apparent diversity of GRSP (Bolliger et al., 2008; Wright et al., 1998). Contradicting their glycoprotein nature, freeze dried GRSP extracts contained more protein-peptide signals with fewer carbohydrate signals, suggesting that it was a 'chaperon containing thioredoxin' (Gillespie et al., 2011).

GRSP consists of a broad range of elements, functional groups and composite substances (He et al., 2010; Lovelock et al., 2004a; Nichols and Wright, 2004, 2006; Nichols, 2003; Rillig et al., 2001b; Schindler et al., 2007; Wang et al., 2015; Wright and Anderson, 2000; Wright and Upadhyaya, 1998) (Fig. 2). Besides C, N, H and O, it also contains Fe, P, Al, Na, Ca, K, Mg and Si. Seven dominant functional groups such as aromatic, aliphatic, carboxyl and carbohydrate type C, along with proteins and carbohydrates are prevalent (Wang et al., 2015). The basic chemical structure (Fig. 2) contains functional groups that are identified through fluorescencing in UV light (Wang et al., 2015). However, the complex nature of GRSP structure still warrants a more detailed examination (Holátko et al., 2021). When released from hyphae, GRSP display a high degree of hydrophobicity and floats on the water surface before binding to mineral or organic particles (Nichols and Wright, 2004). Typically, when sand-based cultures are immersed, GRSP forms a brown foam on the water surface (Nichols and Wright, 2004).

GRSP exist in soil mainly as easily extractable (EE) and total-GRSP (T-GRSP), analytically differentiated by their extraction procedures (Wright and Upadhyaya, 1996) (Table 1). The EE-GRSP is recently produced GRSP fraction with high immunoreactivity and solubility in water, and thus is more labile than T-GRSP (Wright and Upadhyaya, 1998). EE and T-GRSP increase with increasing AMF colonization and AMF-specific fatty acid signatures (phospholipid fatty acid 16:1ω5cis) (Agnihotri et al., 2018, 2021).

2.2. Analyses of GRSP in soil

GRSP were initially detected as a dark red to brown compounds in soil, whereas the brown color was associated with iron (Wright and Upadhyaya, 1998). The EE-GRSP and T-GRSP pools are extracted by autoclaving the soil with alkaline citrate buffer followed by centrifugation (Wright and Upadhyaya, 1996). The molarity of citrate buffer and the autoclaving duration determine the GRSP pool and can be extracted (Table 1). The T-GRSP, being recalcitrant, requires 50 mM citrate buffer (pH 8.0) and prolonged autoclaving. The extraction of T-GRSP is repeated until a straw-colored or slightly colorless extract is obtained. This requires up to seven cycles (Wright and Upadhyaya, 1996, 1998) of autoclaving and centrifugation with citrate buffer. The yellow color of the extract indicates an inherent non-specificity of the extraction method: some fulvic- and humic-like substances are also co-extracted at pH 8.0. The EE-GRSP pool is extracted with 20 mM sodium citrate buffer (pH 7.0) followed by centrifugation (Nichols, 2003; Wright and Upadhyaya, 1998). Unlike T-GRSP, one extraction cycle is sufficient to obtain the EE-GRSP pool.

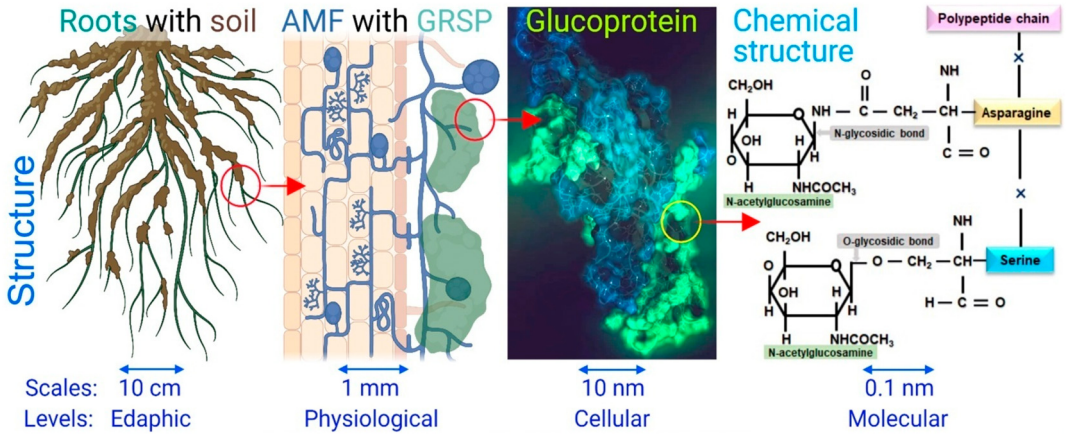

Fig. 1. Localization of glycoproteins (glomalin related soil proteins, GRSP) on roots and arbuscular mycorrhizal fungi (AMF), and chemical structure. Between each of the four levels there is a scaling of 100 times. Chemical structure of a typical glycoprotein consisting of amino sugars, N- or O-glycosidic bonds and polypeptide chain. The × between amino acids shows the possibility of various lengths of polypeptide chain. Edaphic, physiological, cellular and molecular levels are presented. (Created with BioRender.com).

Despite efforts to purify GRSP by precipitation with trichloroacetic acid, many non-protein impurities have been detected in the extracts (Gillespie et al., 2011; Schindler et al., 2007). No acid-free glomalin was obtained by extracting GRSP either before or after humic acid extraction that interferes with GRSP quantification (Moragues-Saitua et al., 2019).

The Bradford protein assay and enzyme linked immunosorbent assay (ELISA) are used to quantify GRSP against the background of various other compounds extracted by Na-citrate buffer (e.g., fulvic acids) (Table 1). Recovery in the indigenous state is hindered by the adsorption and desorption of GRSP on various sorbents (Jia et al., 2016), and strong binding with soil components that includes clays, amorphous and crystalline sesquioxides, organic matter fractions such as humic and fulvic acids (Fig. 3). The GRSP sorption depends on soil pH, organic matter and clay contents (Churchman et al., 2006; Jia et al., 2016; Paterson et al., 1991). These properties are critical to analyze before studying GRSP. Due to the differences in soil chemistry, the universal protocol for GRSP extraction does not ensure its recovery in the native state because organic compounds (e.g., fulvic acids) are co-extracted, particularly in soils enriched with organic matter (Nichols and Wright, 2005). Many other plant-derived glycoprotein sources such as polyphenolic compounds and humic acids cross-react with the Bradford reagent, leading to the misinterpretation of the real GRSP content (Jorge-Araújo et al., 2015; Whiffen et al., 2007). The covalent bonds generated between proteins and polyphenolic compounds during extraction make GRSP extraction and quantification difficult and partly uncertain (Jorge-Araújo et al., 2015). The GRSP measured through the Bradford protein is discussed in terms of fungal origin and the age of

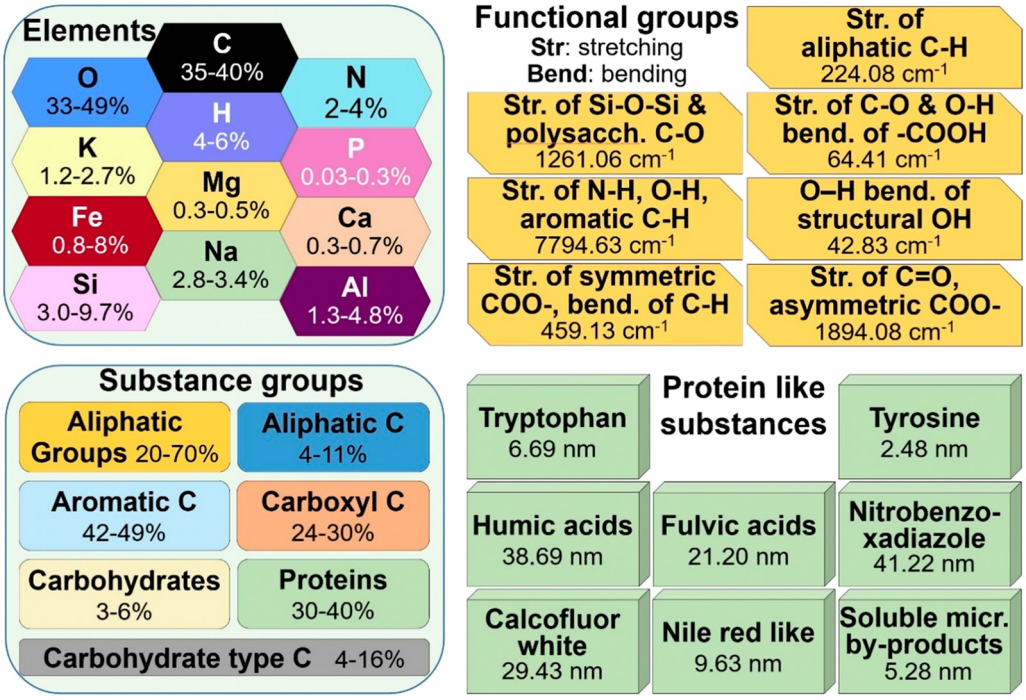

Fig. 2. Chemical structure and composition of GRSP (cm^{-1} indicates wave number, i.e., units of IR spectra, and nm indicates the Excitation-Emission Matrix (EEM) wavelength range of the fluorescence spectra produced by X-ray photoelectron spectroscopy, XPS) (He et al., 2010; Lovelock et al., 2004a; Nichols and Wright, 2004, 2006; Nichols, 2003; Rillig et al., 2001b; Schindler et al., 2007; Q. Wang et al., 2015; Wright and Anderson, 2000; Wright and Upadhyaya, 1998) (for details see Table S2).

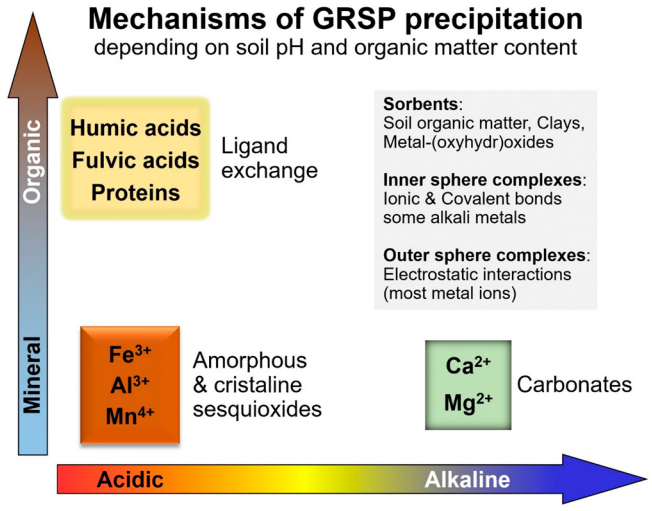

Fig. 3. Precipitation and sorption mechanisms of glomalin related soil proteins (GRSP) released from AMF hyphae in soil: the most common sorption on specific substances in soils depending on soil pH and organic matter content. GRSP is strongly bound to organic matter, sesquioxides and clay minerals. Outer sphere and inner sphere complexes are formed with GRSP. GRSP is released faster from the outer than from the inner sphere complex due to the strong bonds in the last one (Churchman et al., 2006; Jia et al., 2016; Paterson et al., 1991).

the EE and T-GRSP pools (Staunton et al., 2020; Whiffen et al., 2007). GRSP are operationally defined based on the extraction method and therefore recent studies have refined the terms such as autoclaved citrate extractable (ACE) protein and citrate extractable soil proteins (CESP) as more appropriate to designate GRSP (Holátko et al., 2021; Hurisso et al., 2018) (Table 1). This calls for better and unified methods to identify and quantify GRSP based on other organic compounds including proteins (Roberts and Jones, 2008). ELISA using monoclonal antibody Mab32B11 is a better method to quantify GRSP (Wright et al., 1998; Wright and Upadhyaya, 1996). However, impurities of plant origin may replace GRSP and bind to the microtiter plate hindering the GRSP quantification (Otten et al., 1997; Rosier et al., 2006). A modified Lowry method that yields separate measurements for protein and polyphenols has also been recommended for GRSP estimation (Redmile-Gordon et al., 2013). However, the Bradford assay remains a preferred method for GRSP estimation over the Lowry approach. The interference caused by polyphenols and other compounds is less likely to be encountered in soils with low organic matter content (Agnihotri et al., 2021). To improve the accuracy of the Bradford assay for GRSP measurement, modifications have been suggested such as protein estimation using the dilution curve of the extract that includes the differential sensitivity towards Coomassie brilliant blue-250 (CBB) (Moragues-Saitua et al., 2019). However, the Bradford protein assay may over estimate GRSP due to the possible cross-reactivity of Coomassie brilliant blue dye with substances of plant origin and humic-acid like compounds that cannot be ignored (Holátko et al., 2021; Moragues-Saitua et al., 2019). Another study suggested that extract dilution and subtracting the pH-regulated absorbance prior to quantification enables to improve the precision of Bradford assay to estimate GRSP content in organic matter rich forest soils (Cissé et al., 2020).

3. Functions of glycoproteins

3.1. Functions of GRSP for AMF

GRSP share some properties with the fungal hydrophobins and shield hyphae from nutrient losses (Wessels, 1996). A conceptual model proposed in 2007 identified three components of GRSP with the following functions: i) as chaperonins at the cellular level, ii) as hyphal wall components at the AMF physiological level, and iii) as soil-aggregating substances at the edaphic level. The presence of GRSP in the hyphal cell walls has also been related to reduced mycelium palatability for fungal grazers (Purin and Rillig, 2007). GRSP mitigate salinity stress (Hammer and Rillig, 2011), sharing similarities with heat shock protein 60 (Hsp60) (Gadkar and Rillig, 2006). GRSP are also involved in mitigating the cytosolic damage of sodium-induced protein misfolding (Hammer and Rillig, 2011; Maathuis and Amtmann, 1999). To ease the hyphal proliferation through aggregates, AMF increases GRSP production under abiotic stress conditions, e.g. droughts. Even though water-limiting conditions had adverse effects on living AMF biomass (colonized roots and hyphae), the GRSP fractions (EE-GRSP and T-GRSP) increased along with portion of water-stable aggregates (0.25-1 mm) (Zou et al., 2013).

Together, GRSP protect AMF hyphae from drought and salinity stress as water-holding and lubricating substances, provide turgidity and flexibility for the cell walls, and form protective coatings for hyphae and aggregates. We speculate that the high moisture within GRSP gel under drought is the wet channel, through which nutrients move to the roots and to AMF hyphae even at low water content in bulk soil.

3.2. Contribution of AMF and GRSP to soil C sequestration

3.2.1. Direct contribution of AMF hyphae and GRSP to C sequestration in soil

The direct contribution of mycorrhiza to C accumulation in soil can be summed up in three process groups: i) formation and deposition of mycorrhizal residues, ii) release of oxidative and hydrolytic enzymes by mycorrhiza mediating the decomposition of plant and microbial residues as well as SOM, and iii) stimulation of plant growth (Treseder and Holden, 2013). AMF increases plant growth which translates into increased biomass above- and belowground, and increases the C input in the soil (especially by roots and rhizodeposition) (Jones et al., 2004; Treseder and Holden, 2013; Zhou et al., 2020). The two types of AMF hyphae include runner hyphae and absorptive hyphae (Fig. 4). The runner hyphae grow into the soil, infect other roots and connect the surrounding roots with hyphal bridges, and reside in the soil for a few weeks (Friese and Allen, 1991; Zhu and Miller, 2003). Absorptive hyphae are short-lived (5-7 days) and are characterized by dichotomous branching (Fig. 4), subsequently developing a fan-shaped network (Friese and Allen, 1991; Staddon et al., 2003). Although it remains unknown which hyphal pool is associated with larger GRSP amounts, the coarse hyphae clearly contain more GRSP than finer ones (Lovelock et al., 2004b).

The mean residence time (MRT) of C stored inside the aggregates does not exceed the MRT of C stored by soil-GRSP complex, whereas the resistant chitinous materials (amino sugars) of the hyphal cell walls is responsible for C accumulation (Chen et al., 2021; Cui et al., 2020; Zhu and Miller, 2003).

The GRSP contribution to total C is larger than that of microbial biomass and that of hyphal biomass (Rillig et al., 2001b). In the upper 0-10 cm soil depth, GRSP typically contains 5% of total N and 3.2% of total C (Lovelock et al., 2004a) (Table S2). This is a very large GRSP contribution to the soil C and is common in natural ecosystems, whereas a higher ratio of T-GRSP to SOC is common in grasslands (Bai et al., 2011).

3.2.2. Indirect contribution of AMF hyphae and GRSP to SOC sequestration

The indirect contribution of GRSP to C sequestration is crucial because it operates mainly through soil aggregation (Miller and Jastrow, 2000) and consequently, occluding organic compounds from plant and microbial necromass (Awad et al., 2013) protects them from microbial and enzymatic attacks (Fig. 4). The indirect effects of GRSP on SOC sequestration include the formation and stabilization of aggregates resulting in increased C sequestration through i) physical protection of SOC, ii) better plant growth and deeper root growth at the site of AMF spores, iii) increased microbial activity by contributing to active C pools (Subramanian et al., 2019; Wright and Upadhyaya, 1998), and

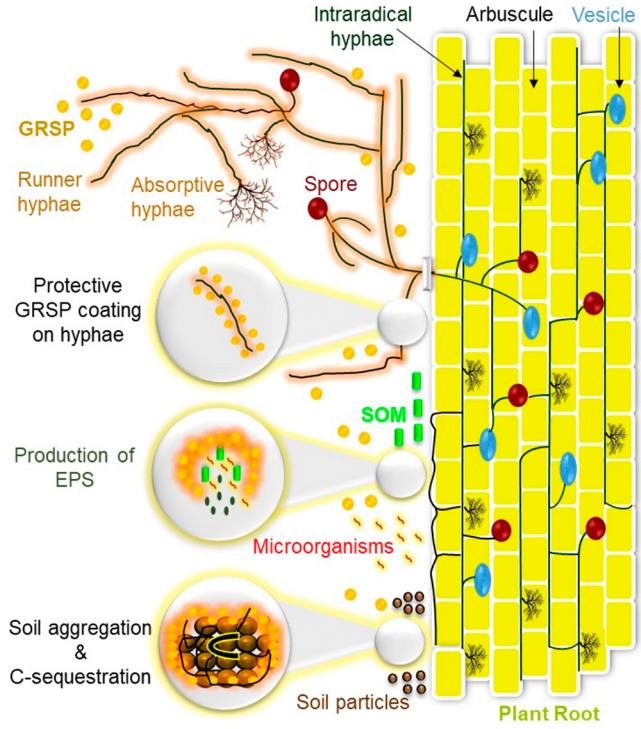

Fig. 4. Glomalin related soil protein (GRSP) production on hyphae, arbuscular mycorrhizal fungi (AMF) infectious propagules, i.e., arbuscules, spores, vesicles, intraradical and extraradical (absorptive and runner) hyphae. The three principal functions of GRSP in soil are presented in loupes: 1) forming a protective coat on hyphae (to prevent nutrient loss), 2) production of microbial extracellular polysaccharides (ESP), and 3) soil aggregation through the binding of soil particles together by AMF hyphae and GRSP and C sequestration therein.

iv) increasing locally soil moisture during drought periods, similarly to root mucilage (Carminati et al., 2011).

AMF contributes to C sequestration by translocating exudates away from the rhizosphere – the zone of higher microbial activity and from respiratory zones in the soil matrix (Treseder and Allen, 2000; Zhu and Miller, 2003). Moreover, AMF stabilizes the soil structure by markedly increasing the SOC content and the mean weight diameter of aggregates (Xu et al., 2014). GRSP sorbed on the organic substances, clays and silt particles, and AMF hyphae mechanically bind particles thereby enabling aggregate formation and stabilization (Comis, 2002; Rillig et al., 2002a). The second role of AMF is to produce GRSP and also to increase plant growth by improving soil structure, deep root growth, aeration and improving soil moisture status. In doing so, AMF ensures its own survival (Rillig and Steinberg, 2002; Wright and Upadhyaya, 1998). Assimilate allocation to AMF increases nutrient uptake by plants and consequently photosynthetic activity and generates a sink for active C (e.g. carbohydrates), concomitantly increasing microbial and enzymatic activity and available C in the soil (Sommer et al., 2017; Subramanian et al., 2019).

Contradicting its hydrophobic nature, GRSP could contribute to dissolved organic C pool (Singh et al., 2017). GRSP also increases C sequestration by maintaining labile C compounds within the aggregates and reducing the degradation of available organic matter (Rillig, 2004).

3.3. Role of GRSP in C sequestration depending on physical and biochemical soil properties

Three principal mechanisms are responsible for SOC stabilization: physical protection, chemical and biochemical stabilization (Six et al., 2002). The physical protection by AMF involves the formation of a 'sticky-string bag' by the co-action of roots and hyphae binding soil particles together to form micro- and macroaggregates (Miller and Jastrow, 2000; Yudina et al., 2018). Binding agents are critical to each of the mechanisms listed above. Based on the mean residence time and relative contribution to SOC, three classes of binding agents can be distinguished i) transient/labile (microbial and plant-derived), ii) temporary (roots and hyphae), and iii) persistent (humified organic matter, polyvalent metal complexes, aluminosilicates and sesquioxides) (Miller and Jastrow, 2000; Gupta, 2011; Tisdall and Oades, 1982; Yudina et al., 2018). AMF belongs to the second category of binding agents and confers to temporary stabilization of macroaggregates (Tisdall and Oades, 1982; Yudina et al., 2018; Zhang et al., 2016). GRSP belong to the third category of binding agents, viz., persistent binding agents (Wright and Upadhyaya, 1996) through active contribution to micro- and macroaggregate formation and stabilization (Nichols and Halvorson, 2013). The aggregate hierarchy concept (Tisdall and Oades, 1982) explains the steps of aggregate formation, with GRSP as integral parts/components of aggregate-binding agents. The GRSP content positively correlates with aggregate stability (Nautiyal et al., 2019; Wright and Anderson, 2000; Wu et al., 2014) as well as with water-stable aggregates of 0.25-0.50 mm diameter (Wu et al., 2012). GRSP facilitates adhesion between and within microaggregates (Wright et al., 2007). Thus, the microaggregates bind together into macroaggregates (>250 mm) by forming a mechanical framework of macroaggregates through AMF roots and hyphae, but also by microbial- and plant-derived transient/labile binding agents (Kleber et al., 2007; Six et al., 2002; Totsche et al., 2018). Hence, AMF increases SOM residence time by stabilizing macroaggregates (Miller and Jastrow, 2000).

Iron constitutes a considerable portion of GRSP (Table S2, Fig. 2) and is responsible for its typical red-brown color (Wright and Upadhyaya, 1998). Iron also converts monomeric GRSP units into a multimeric complex and is involved in creating a folding pattern in the protein to intensify the hydrophobic interactions between the monomeric units (Nichols, 2003). Phytopathogenic fungi have reduced access to iron when sequestered within GRSP molecules (Rillig et al., 2001b). Although iron remains central to most studies with GRSP and metal ions, other polyvalent cations (Al^{3+}, Ca^{2+}, Mg^{2+}) probably have similar effects on GRSP structure and stabilization.

GRSP have been specifically related to β-glucosidase activity and carbohydrate content. Similar to extracellular polysaccharides (EPS), GRSP act as a sticky and insoluble biofilm that glues together organic matter, clays, minerals, (oxyhydr)oxides, and microorganisms (Costa et al., 2018; Martinez-Salgado et al., 2010; Redmile-Gordon et al., 2014; Wu et al., 2012). The resulting microenvironment enables microbial degradation of organic matter and produces EPS for additional aggregate stabilization (Awad et al., 2013; Wright and Upadhyaya, 1998) (Fig. 4). The EPS function is to support plants with water and nutrients and to protect against drought stress (Carminati et al., 2011; Costa et al., 2018). The labile organic compounds (such as polysaccharides) and persistent binding agents (humic-like acids, aluminosilicates, crystalline oxides) stabilize microaggregates (Tisdall and Oades, 1982; Yudina et al., 2018). GRSP contains up to 85% polysaccharides that are resistant to microbial decomposition, and therefore, are involved in binding mineral and organic particles to aggregates for long periods (Gunina and Kuzyakov, 2015). Hence, independent of origin (roots, hyphae, bacteria), GRSP strongly influence the physical and biological soil properties (Ahmed et al., 2018; Majumder and Kuzyakov, 2010). Soil aggregation and stabilization facilitated by GRSP and AMF can be summarized into the following steps: i) adhesion within and between microaggregates by GRSP, ii) microaggregate stabilization by labile organic compounds (extracellular polysaccharides) produced under the influence of GRSP, iii) the binding of microaggregates to form macroaggregates by AMF hyphae and plant roots, iv) aggregate stabilization by bridging the gaps within aggregates by organic agents such as GRSP, and v) the formation of a protective coat of GRSP on macroaggregates (Miller and Jastrow, 2000; Wright and Upadhyaya, 1998).

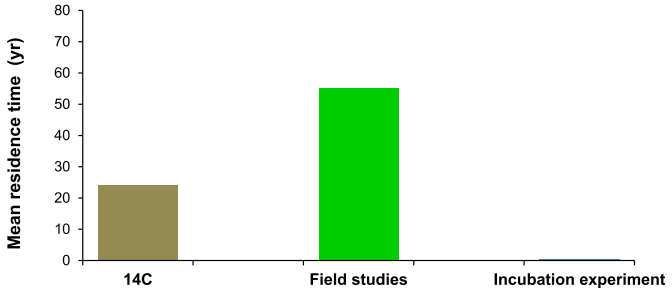

Fig. 5. Mean residence time (MRT) of glomalin related soil proteins (GRSP) in soil. ^{14}C (radiocarbon) dating based on the stock-flow model assumptions of ^{14}C content in GRSP in the O and A horizons of a tropical forest; the MRT of GRSP ranged from 6 to 42 years (Rillig et al., 2001b). Field studies: The conversion of grasslands to arable lands exponentially decreased GRSP content and, after 11-92 years, a steady state equilibrium (when about 39-69% of the original contents remained) was reached (Preger et al., 2007). Incubation experiments: after a 150-day incubation of field soil in dark, GRSP contents decreased by 25% (Steinberg and Rillig, 2003); in a 413-day laboratory incubation of agricultural and native soils, 50% of GRSP remained (Rillig et al., 2003b) (for details see Table S1).

3.3.1. GRSP decomposition and its mean residence time in soil

The recalcitrant nature of GRSP is evident based on their recovery after autoclaving (Wright and Upadhyaya, 1996) and their long residence time in soil (Rillig et al., 2001b). GRSP residence time in soils under field conditions is between 6 and 42 years (Fig. 5, ^{14}C based), which confirms the medium to long GRSP storage (Rillig et al., 2001b). This MRT of GRSP is similar to that of the total SOM of 50-60 years (Schmidt et al., 2011; Zang et al., 2018). Because GRSP contains 2-4% N, it is prone to microbial attacks and mineralization to reduce N limitation in soil (Treseder and Turner, 2007). In incubation experiments, however, the GRSP content decreased much faster, e.g. by 25% over 150 days whereas the hyphal length decreased by 60% (Steinberg and Rillig, 2003). After 413 days incubation, 50% GRSP was still present in agricultural and forest soils, indicating its high resistance to decomposition (Rillig et al., 2003b).

GRSP loose immunoreactivity after sloughing off from hyphae and with increasing hyphal age. Accordingly, immunoreactivity is a common characteristics of the newly produced GRSP (Wright and Upadhyaya, 1998). Among all GSRP fractions, the EE-GRSP and T-immunoreactive soil proteins were lost most rapidly before reaching a steady state between production and decomposition (Preger et al., 2007). Over the years, GRSP accumulation in soil represented a substantial GRSP absorption to SOM (10-100 g C m^{-2} yr^{-1}) (Treseder and Turner, 2007). This governs C sequestration, especially in forests soils (Zhang et al., 2017). The recalcitrance indices (the ratio of the sum of alkyl and aromatic C, over the totality of O-alkyl C and carboxyl C) were approximately 2 times higher in GRSP than in SOM (Zhang et al., 2017).

4. Factors affecting GRSP production and release

Several climatic, biotic and soil factors influence GRSP production and release by AMF (Fig. 6). The GSRP content in soil is regulated by the balance between its production by AMF and its microbial decomposition. GRSP production largely depends on the assimilates that AMF receives from the host plants (Treseder and Turner, 2007). After being released into the soil, the GRSP fractions lose their immunoreactivity (Nichols and Wright, 2004).

GRSP production and AMF-mediated aggregate formation and stabilization depend on a broad range of conditions (Fig. 6): i) climate (temperature, precipitation and drought frequency) (Wang et al., 2020), ii) season, which can influence AMF biomass (He et al., 2010), iii) soil properties (structure, texture, pH, electrical conductivity, nutrient and water status, iron and phosphorus content, organic matter type and content, as well as polyvalent cations that influence AMF hyphal growth), iv) various cycling processes: wetting and drying; freezing and thawing; clay shrinking and swelling, v) architecture and morphology of hyphae and roots, vi) AMF species, vii) AMF metabolic products (their diffusion and persistence), viii) plant biomass and belowground assimilate allocation, rhizodeposits, litter amount and quality, and ix) soil management history that includes vegetation, tillage and cropping systems (Comis, 2002; He et al., 2010; Lovelock et al., 2004b;

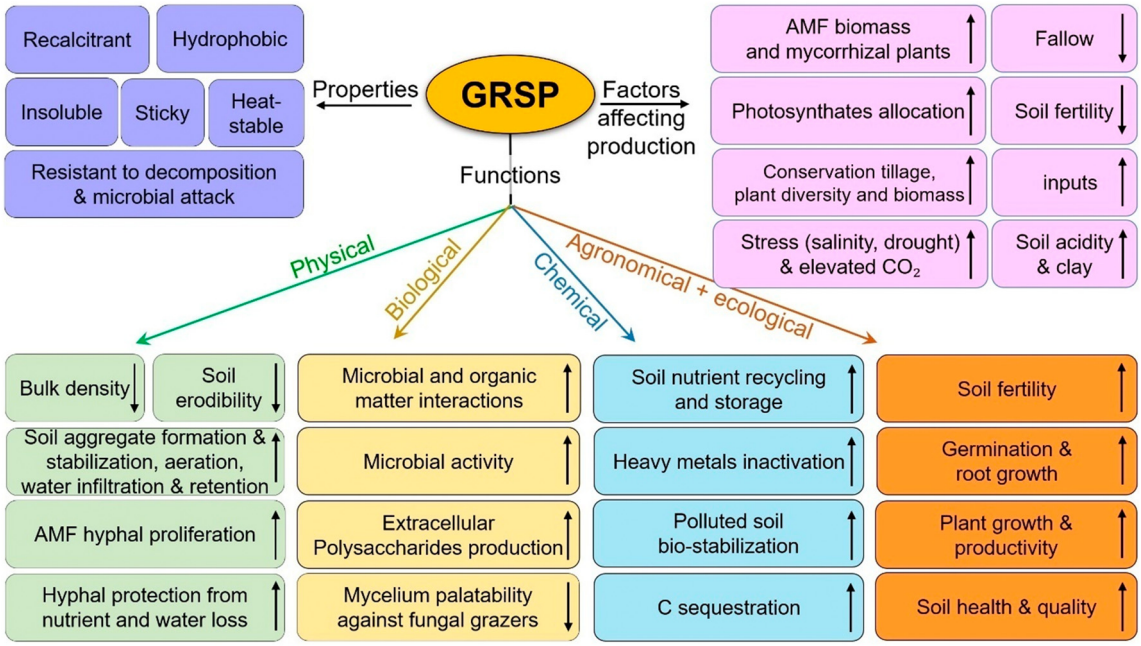

Fig. 6. An overview of glomalin related soil proteins (GRSP) functions, properties and factors affecting its production. These GRSP properties complicate their extraction from soil. Factors are responsible for increasing/decreasing GRSP production (↑↓). The physical functions of GRSP for protection of soil aggregates, AMF survival and growth promotion. The biological functions of GRSP are related to soil health improvement. The chemical functions of GRSP lead to soil biostabilization and agronomical functions in relation to plant growth. For Factors: the arrows show the effect of each factor on GRSP production; for Functions: the arrows show the effect of GRSP on specific function.

Miller and Jastrow, 2000; Nichols, 2003; Rillig et al., 2002a; Treseder and Turner, 2007; Wang et al., 2020) (Fig. 6).

4.1. Effects of climate

Temperature and precipitation are especially important parameters for GRSP production and decomposition (Wang et al., 2020). Low temperatures inhibit AMF hyphal decomposition (Miller et al., 1995) and ensure continued GRSP production. Higher temperatures, stimulate microbial activity which accelerates organic matter mineralization, while GRSP become susceptible to microbial attacks, loose its immunoreactivity and thereby, its content decreases (Adame et al., 2012; Comis, 2002). Although higher temperatures increase the C allocation to AMF by plants, and subsequently increases the AMF biomass, warming decreases the immunoreactive GRSP content and aggregate stability due to higher microbial activities decomposing GRSP (Rillig et al., 2002b).

Microbial processing of GRSP results in i) increased solubilization and ii) decreased sorption on mineral particles (Steinberg and Rillig, 2003). EE and Total-GRSP content decreases with increasing soil moisture (Vasconcellos et al., 2016). However, in littoral (intertidal zone) seagrass meadows, GRSP increases along with high annual rainfall during the rainy season (Adame et al., 2012). Climatic factors such as temperature and precipitation accounted for 29% and 20% of variations in GRSP accumulation in sub- and topsoil, respectively (Wang et al., 2017).

GRSP production is seasonally dependent; AMF biomass peaks in the spring and summer, and consequently, GRSP strongly increases in the summer (Emran et al., 2012; He et al., 2010). As a result, the EE-GRSP increased more than the T-GRSP from spring to autumn (Turgay et al., 2015). Stress conditions such as drought stimulate GRSP production as a byproduct of the plant survival strategy by increasing the assimilate allocation to AMF (Emran et al., 2012). Producing GRSP, AMF promotes aggregation to enable hyphal proliferation (Rillig and Steinberg, 2002). This, in turn, enables better and deeper root growth and AMF proliferation and thereby increases the AMF-mediated nutrient allocation to the plant. These mechanisms are crucial to the survival of both symbiotic partners.

4.2. Effects of elevated CO_2

Elevated CO_2 levels increase AMF colonization and GRSP content (Rillig et al., 2000) due to induced nutrient-limiting conditions for plants belowground against the background of C excess aboveground (Kuzyakov et al., 2019). Hence, more assimilates are allocated for AMF growth and invested in GRSP production (Haddad and Sarkar, 2003; Treseder and Turner, 2007) to mine for N and P. The active plant-AMF symbiosis under elevated CO_2 produces fresh immunoreactive GRSP on young hyphae (Haddad and Sarkar, 2003).

4.3. Effects of soil properties and nutrient content

4.3.1. Soil physico-chemical properties

Various soil physico-chemical properties affect GRSP content with the following decreasing intensity: bulk density > pH > electrical conductivity (Z. Zhang et al., 2017). Total and EE-GRSP contents decrease with increasing bulk density (Vasconcellos et al., 2016). Well aggregated soils have a lower bulk density, support AMF growth and therefore, a higher GRSP content (Zhong et al., 2017). The GRSP content in soils is associated with organic matter and clay contents (Nichols and Wright, 2005). A lower GRSP content is common in iron-deficient calcareous soils and soils with carbonate as the aggregate binding agent (Rillig et al., 2003a; Wright and Upadhyaya, 1998).

Soil pH influences both the GRSP composition and content (Wang et al., 2014) because of the strong effect of soil acidity on AMF. Among the soil types, acidic Ultisols have the highest GRSP content that decreases with increasing soil pH (Wang et al., 2014). The GRSP decomposition rate in acidic soils is slow because Fe and Al sesquioxides increase its resistance to degradation. Soil salinity decreases the GRSP content (Kohler et al., 2010). Although GRSP reduces salinity stress for AMF, NaCl concentrations beyond a threshold of 150 mM decreased the GRSP content (Hammer and Rillig, 2011). Even in reclaimed coastal land, salinity decreased the AMF biomass and GRSP content (Krishnamoorthy et al., 2014). Highly saline soils not only decrease the GRSP content but also changes the GRSP structure, i.e., higher N, lower C and lower C—O and Si-O-Si functional groups (Zhang et al., 2017).

Soil pH and bulk density directly influence GRSP content, whereas electrical conductivity and soil moisture affect GRSP indirectly through pH and the bulk density (Zhong et al., 2017). Infrared functional groups (IR-II, IRV) and fluorescent substances (tyrosine-like and humic acid-like) are also directly affected by soil moisture, pH and electrical conductivity, thus affecting GRSP composition (Zhong et al., 2017).

4.3.2. Soil nutrient contents

The GRSP content is generally larger in soils with low fertility (Lovelock et al., 2004a). A high soil P content decreases AMF colonization (Sharma and Adholeya, 2015) and the EE-GRSP content (Lovelock et al., 2004a). The GRSP content decreases with increasing Ca, Mg, P and K levels, which are high soil fertility indicators (Lovelock et al., 2004a). In contrast, the GRSP increases with the indicators of lower soil fertility such as high C:N ratio, Al and Fe contents (Lovelock et al., 2004a). However, increasing GRSP content with increasing SOC, total N, available P and K have also been observed (Šarapatka et al., 2019).

The reasons for higher GRSP production in low-fertility soils are i) increased AMF colonization and growth, corresponding to larger assimilate portion allocated belowground, ii) increased GRSP production per AMF unit, iii) persistent hyphae, iv) slower GRSP decomposition, and v) a shift towards AMF communities that produce a larger hyphal biomass and more GRSP than the other species (Lovelock et al., 2004a). GRSP is also important for nutrient cycling because it provides good conditions for microbial enzyme production and increases the activities of acid phosphatase, urease, dehydrogenase, and β-glucosidase (Vasconcellos et al., 2016; Wu et al., 2012). GRSP have therefore been used to assess soil fertility and degradation (Bedini et al., 2007; Šarapatka et al., 2019). The immunoreactive fraction that confers GRSP their sticky nature and strongly increases with the carbonate content and inorganic C/N ratio (Haddad and Sarkar, 2003).

4.4. AMF species

AMF species have various gene sequences responsible for the GRSP production and for specific GRSP functions such as the aggregation efficiency (Magurno et al., 2019). *Glomus* species differ from other genera in their response to nutrient addition and C requirements. They flourish under N fertilization and increase under elevated CO_2 (Egerton-Warburton and Allen, 2000; Rillig et al., 2001a; Rillig et al., 2000). Thus, the lower C requirements of *Glomus* species decrease the GRSP production, which requires substantial C investment by AMF (Lovelock et al., 2004b; Rillig et al., 2001b).

5. Effects of land use on GRSP production

Agricultural practices influence GRSP production (Fig. 7) because the growth and proliferation of AMF communities depends on fertilization, land use, crops, farming practices and disturbances by tillage. Reduced phosphorus fertilization and absence of tillage are the key factors for high AMF abundance and undisturbed GRSP production (Nichols and Wright, 2004). The GRSP content across all soil horizons was highest in forest soils and lowest in agricultural soils under corn and soybeans (Rillig et al., 2003b). The prairie ecosystem had up to 111 m cm^{-3} soil hyphal lengths (475 μg cm^{-3} hyphal dry biomass), whereas pasture had 81 m cm^{-3} soil (339 μg cm^{-3} hyphal dry biomass) (Miller et al., 1995).

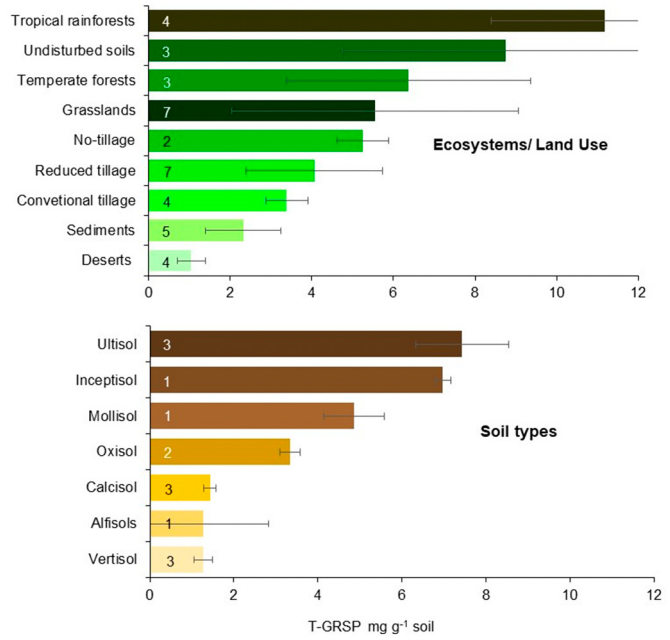

Fig. 7. Total GRSP (T-GRSP, mg g^{-1} soil) content depending on ecosystems, land use and tillage systems (top), and soil types (bottom). Values are presented as mg g^{-1} and are the means ± standard errors of the contents reported in various studies. Numbers of individual studies are indicated in each bar. GRSP content in soil type is presented as averaged between management and cropping systems. Lighter shades represent less content. Data are collected from studies referred in Supplementary Table 3.

5.1. Tillage practices

Tillage destroys AMF hyphae, reduces AMF species richness (Dai et al., 2015; Oehl et al., 2003) and thus reduces GRSP production. Soil mixing during tillage mechanically disrupts and damages the AMF hyphal network. No-till as well as minimum tillage practices, crop rotations and diversified cropping systems increase AMF and contribute to higher GRSP production in the same growing season and in subsequent years. It was reported that no-tillage plots have higher GRSP content and larger aggregates than chisel tillage or intensively tilled organic plots (Wright et al., 2007).

No-tillage retains a higher AMF biomass in terms of root colonization and AMF spore density compared to conventional tillage (Borie et al., 2006; Castillo et al., 2006; Lu et al., 2018). AMF propagules and GRSP content increases in plots without tillage for 6 years than in plots with conventional tillage and in those with reduced tillage (Curaqueo et al., 2011). Thus, conservation tillage maximizes AMF growth, GRSP production, and improves the soil structure (Wilkes et al., 2021). Undisturbed soil maintains a stable hyphal network and consequently strengthens the GRSP-mediated aggregate formation and stabilization.

A continuous GRSP production can be achieved by preventing disruption of the hyphal network (Wright and Upadhyaya, 1998). For example, the abandonment of agricultural land to forest succession increases SOC stocks (Kurganova et al., 2014; Ovsepyan et al., 2019), and discontinued use of agricultural land reinstates GRSP (Liu et al., 2020). Thus, intensive land use, tillage and fertilization decrease AMF formation and GRSP production, whereas its content strongly increases under natural ecosystems, especially under forests.

5.2. Crop rotation and farming practices

Rotation with mycotrophic hosts maintains AMF live biomass, increases GRSP content and improves plant growth (Selvakumar et al., 2018). In contrast, AMF populations decrease following non-mycorrhizal crops (e.g. members of Brassicaceae family such as cauliflower, cabbage, rapeseed) and shortening the fallow periods (Comis, 2002). Plots with diverse plant species have a higher GRSP content than monocultures (Burrows, 2014). Inclusion of Nitrogen-fixing leguminous crops such as chickpea in the crop rotation increases rhizodeposition, this subsequently stimulates AMF growth and GRSP production. Hence, systems with a pearl millet-chickpea had a higher GRSP content than a pearl millet-wheat system (Singh et al., 2018). Among the crop combinations such as wheat, corn, proso millet, and sunflower, the most successful system that produces high GRSP content was in wheat-corn-proso millet managed with no-till (Wright and Anderson, 2000). Sorghum-wheat-soybean rotation under no-tillage harboured a higher microbial community richness, total organic carbon (TOC), as well as carbohydrate and GRSP pools as compared to continuous conventional tillage (González-Chávez et al., 2010). This sorghum-wheat-soybean rotation system was therefore considered as the best practice to increase SOC sequestration. The GRSP content in mycorrhizal-inoculated plants (higher in maize than soybean) grown under organic management practices was larger than in a non-inoculated soybean-maize cropping system managed with organic practices and mineral fertilization (Agnihotri et al., 2014).

Organic farming supports AMF diversity (Oehl et al., 2004). In comparison to conventional systems, organic farming (amended with manure and compost) increased AMF abundance, species richness and diversity as well as Bradford reactive and immunoreactive soil proteins (Turgay et al., 2015; P. Wang et al., 2015). Consequently, organic inputs increased the portion of macroaggregates and the mean weight diameter of aggregates in parallel with increasing microbial biomass, organic C and the GRSP fractions (Zhang et al., 2014). Similarly, organic orchards also contained a higher AMF species richness and T-GRSP than conventional orchards (Song et al., 2019). Long-term application of poultry, pig or cattle manure (Bertagnoli et al., 2020; Guo et al., 2019), and the application of compost or farmyard manure also increases GRSP content (Turgay et al., 2015).

5.3. GRSP in sediments

GRSP can be occluded with clay particles into eroded out into the rivers, thus contributing to sediment structuring and serving as a nutrient source for marine organisms (Harner et al., 2004). A higher GRSP accumulation in the sediment below a *Posidonia oceanica* seagrass mat than in the mat itself suggests a reclamation of sediment quality and anoxic environment that prevents GRSP degradation (Lopez-Merino et al., 2015). Owing to its C-sequestration potential, GRSP could be a tracer or biomarker for terrestrial-marine transport compared to other biological, chemical and biochemical tracers (Adame et al., 2012). In floodplain soils, as determined through the relationship with site age, GRSP had a turnover time of 35 years (Harner et al., 2004). The AMF contribution to long term SOC sequestration in sediments was evident from the close positive correlation between GRSP, AMF spores and SOC content (Wang et al., 2018)Das et al., 2020).

6. Conclusions

1. The AMF production of GRSP is a strategy for survival in less aggregated soils by acting as a particle binding, lubricating, and and water- holding agent. This results in i) improved soil quality, ii) increased water retention and aeration, iii) increased nutrient storage and availability, iv) increased microbial biomass and activities, v) increased activities of nutrient-cycling enzymes such as phosphatases, aminopeptidases, and β-glucosidases, and vi) better and deeper root and hyphal growth.
2. GRSP are heat-stable, sticky and hydrophobic glycoproteins produced on AMF hyphal walls. GRSP are recalcitrant, resistant to microbial attacks and reside in soil for years, enabling long-term C sequestration and aggregate stability. The glycoprotein content in soils ranges up to 15 mg g^{-1} and increases with the clay and organic

matter content as well as acidity, but decreases with salinity and bulk density.

3. The contribution of AMF and GRSP to SOC sequestration involves the following mechanisms i) soil aggregate formation by physically entrapping organic particles, ii) by increasing hyphal biomass, iii) by enhancing belowground plant C-allocation (including root growth) because AMF are obligate symbionts needed assimilates, and iv) GRSP itself works as a C-source. The AMF and GRSP indirectly contributes to SOC sequestration through aggregation, which is by far more important than their direct involvement as a C-source. AMF and GRSP both physically and biochemically stabilize the soil structure.
4. GRSP production increases under i) nutrient-limiting conditions (especially phosphorus limitation) to increase nutrient acquisition and to support better plant growth, ii) stressed conditions such as drought due to the resemblance of their protein sequence with hsp60, iii) drying and rewetting cycles protecting AMF hyphae from nutrient losses, iv) elevated CO_2 due to increased belowground assimilate allocation, especially to AMF, v) soils with poor aggregate stability to increase plant root and AMF hyphal proliferation, vi) diversification of plant species (crop rotation and intercropping) due to host-specific interactions of AMF species, vii) conservation tillage practices due to less hyphal disruption, and viii) organic amendments, which increase AMF biomass.
5. GRSP are not currently included in soil health assessment programs, despite the fact that they are linked to a variety of ecosystem processes and serve as a low-cost proxy for soil quality, and as well as AMF biomass and the success of agricultural management and remediation approaches.
6. To raise awareness among researchers and farmers about the potential of GRSP as a C-sequestration and quality indicator, controlled experiments involving AMF quantification (quantitative PCR assays, AMF-signature lipids, microscopic measurements) and GRSP (ELISA and advanced spectroscopic characterization) followed by field demonstrations are required.
7. Finally, AMF-produced GRSP improves several soil biochemical processes as i) a stress protectant, ii) a soil conditioner, and iii) C sequestration agent, mainly by structuring aggregates, making them more stable and thus, establishing and improving the habitat for roots and microorganisms.

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Ethics approval

This article does not contain any studies with human participants or animals performed by any of the author.

Consent to participate

Not applicable

Consent for publication

All authors agree to submit for publication.

Availability of data and material (data transparency)

Not applicable

Code availability (software application or custom code)

Not applicable

CRediT authorship contribution statement

RA and MPS created an outline, skeleton, prepared the first draft, figures. Revised and finalized the review for submission. AP, AR, SB, AKP, MCM provided intellectual inputs in the earlier drafts. IK has contributed in revising the article. YK contributed in conceptualization of review, provided intellectual inputs, suggested corrections in the drafts, revised and finalized the review draft, figures, tables, supplementary materials. All authors contributed to the article and approved the submitted version.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2021.150571.

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