



## Glomalin and Contribution of Glomalin to Carbon Sequestration in Soil: A Review

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### ABSTRACT

Arbuscular mycorrhizal fungi (AMF) improves the uptake of nutrients and water to the plants through mutual symbiosis. Only AMF produces glomalin related soil protein (GRSP). *Acaulospora morroaiae*, *Glomus luteum*, *Glomus verruculosum*, *Glomus versiforme* are the effective glomalin producing AMFs. Mixed primary forest, tropical rainforest, soil organic matter, clay soil, no tillage, quality and quantity of fertilizers, crop rotation, and water stable aggregates are also suitable to increase glomalin production. Glomalin is a glycoprotein that contains 30–40% carbon (C) which is assumed to be stable and persistent in soil. The glomalin can sequester more carbon in the soil due to its high carbon and aggregate stability. Greater aggregate stability leads to high organic carbon protection in terrestrial ecosystems. The lowest glomalin content (0.007 mg per gram soil) was found in Antarctic region, and the highest glomalin content (13.50 mg per gram soil) was observed in tropical rainforest. In agricultural soil, glomalin content varies between 0.30 and 0.70 mg per gram soil. The GRSP containing soil organic carbon (SOC) in deeper soil layers was 1.34 to 1.50 times higher than in surface layers. Glomalin can sequester 0.24 Mg C ha<sup>-1</sup> in soil when present at 1.10±0.04 mg g<sup>-1</sup>. At elevated CO<sub>2</sub> (700 μmol mol<sup>-1</sup>) level, easily extractable glomalin (EEG) and total glomalin (TG) were 2.76 and 5.67% SOC in the surface soil layer over ambient carbon dioxide (CO<sub>2</sub>) level. This finding indicates the effective function of GRSP C sequestration in soil under global environmental change scenarios. Glomalin can also protect labile carbon that can help regulating nutrient supply to the plants. No tillage practice causes higher AMF hyphal length, GRSP and water stable aggregate (WSA) compared to that of conventional tillage practice. The current review demonstrated that GRSP is an important tool for carbon storage in deep soils. Glomalin mediates soil aggregates, improves soil quality, increases carbon sequestration and crop production, and mitigates climate change.

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### Introduction

Soil organic matter (SOM) improves soil and air quality through increasing agricultural production and improving environmental functions. The SOM also affects the dynamics and bioavailability of plant nutrients, infiltration rate, available water capacity, and the resistance against erosion by water and wind. Sequestered carbons in the soil are used in agriculture, forestry, and reduce ever increased carbon dioxide from the atmosphere (Batjes 1996; Del Galdo et al., 2003; Lal, 2003). There are many ways such as conservation agriculture, minimum or zero tillage, and use of living or dead organic materials to increase SOC in soil. Since 1996 some researchers claimed that AMF mediated glomalin directly as well as indirectly can sequester carbon in the soil. Glomalin owns a plentiful amount of insoluble hydrophobic glycoprotein, which can protect the decomposition of soil organic matter. The GRSP is considered an essential component of the SOC

pool in terrestrial ecosystems (Jia et al., 2016). Understanding the mechanism for controlling the accumulation and stability of soil C is critical to predict the future climate of the earth (Knorr et al., 2005). A recent study shows AMF can only produce copious amounts of insoluble, hydrophobic, recalcitrant glycoprotein, named glomalin. Stable aggregates can store and protect the SOC until the aggregates break down. Protected organic carbons increase with the increase of aggregate stability in soil. Very little information is available regarding glomalin content by different factors and the effect of glomalin on soil quality and crop productivity through sequestration of C and mitigation of climate change. Therefore, this review discusses the effect of different factors on glomalin content and direct and indirect impacts of glomalin on C sequestration in soils, soil health, crop production and climate change.

## Materials and Methods

This review is based on the use of secondary data from different journals, research magazines, scientific reports, books, and proceedings. The review focused primarily on the literature search and restricted to articles and report papers published. The published articles were searched and identified from different electronic databases, author's research article, Web of Science, International system for agricultural science and technology (AGRIS), Research Gate, Science Direct, and Springer. The documents collected were mainly focused on glomalin and the effect of glomalin on soil aggregates and C dynamics in soil and plants. For a critical review, data and literature were compiled and discussed on the effect of AMF species, factors affecting on the glomalin content, carbon pool in glomalin, soil aggregate formation by glomalin, direct and indirect effect of glomalin for carbon sequestration in soil and plant to mitigate the climate change. Using these criteria, 53 studies were found suitable to be included in the review (see references of review). I also complemented this search with references cited in the primary literature. These studies were published over 26 years between 1994 and 2020.

## Results and Discussion

### Factors Affecting Glomalin Content and the Effect of Glomalin on Soil Characteristics

Plant root provides C for growth and reproduction of a ubiquitous group of symbiotic fungi called AMF. Only AMF produces GRSP. The GRSP contains 2.35 – 2.56 times higher in the primary forest than the secondary forest and farmlands (Wang et al., 2015). Different AMF species produce different amounts of glomalin. Among the studied AMF species *Acaulospora morroaiae*, *Glomus luteum*, *Glomus verruculosum*, *Glomus versiforme* produced significant amount of glomalin (Wright et al., 1996). Similar findings were reported by Wright and Upadhyaya (1999). *Acaulospora morroaiae* and *Glomus intraradices* AMF produced the highest and the lowest glomalin contents among the studied *Acaulospora morroaiae*, *Gigaspora rosea*, *Glomus etunicatum*, and *Glomus intraradices* AMF (Lovelock et al., 2004). Management practices such as tillage, quantity, and quality of fertilizers applied, over-grazing, and plant protection strategies impact on AMF viability and community structure (Oehl et al., 2004; Jarecki and Lal, 2005). Wright and Upadhyaya (1998) conducted research in cultivated and undisturbed soils observed that aggregate stability and immune reactive easily extractable glomalin (IREEG) fraction increased in undisturbed soil. Nichols and Wright (2005) reported that native grasses soil contained higher amounts of glomalin than introduced grasses soil as well as after shifted these lands to cattle, glomalin content was higher than over-grazed soils. The GRSP structures and their differences depend on the content of SOC as well as the depth of soil (Wang et al., 2020). Different pools of glomalin such as TG, immune reactive total glomalin (IRTG), EEG, and IREEG directly contribute carbon sequestration in soil (Figure 1). In respect of TG, the decline rate was observed 16.65 and 46.04% in fallow land, and the arable land systems compared to forest land, respectively. On the other

hand, EEG is positively correlated with the amount of C and N in soil. It means the EEG increases with the increase of C and N in soil (Fokrom et al., 2013). Wang et al. (2015) also reported that GRSP content is positively correlated with SOC irrespective of the detailed descriptions of surface and deep soils. Glomalin decreased with the increase of soil depth, and the ration of glomalin to SOC was 1.34 - 1.50 times higher in 80 - 100 cm depth than 0-20 cm depth (Wang et al., 2017). The highest SOC and EEG (36.8 and 0.53) were observed in forest land use, whereas the maximum TG was observed in horticultural land management systems at 0-15 cm soil depth (Figure 2). At 15-30 cm soil depth, the maximum SOC, TG, and EEG (3.62, 4.47, and 0.35) were obtained from the forest land use system. The findings show that SOC decreased with the increase of soil depth as well as forest soil always the highest results in respect of SOC, TG, and EEG except in TG up to 15 cm soil depth. Wang et al. (2020) also reported that AMF produced 1.8–2.0 times higher GRSP up to 40 cm soil layer than at 40–100 cm. GRSP related SOC sequestered 1.2 times higher in deep soil than surface soil.

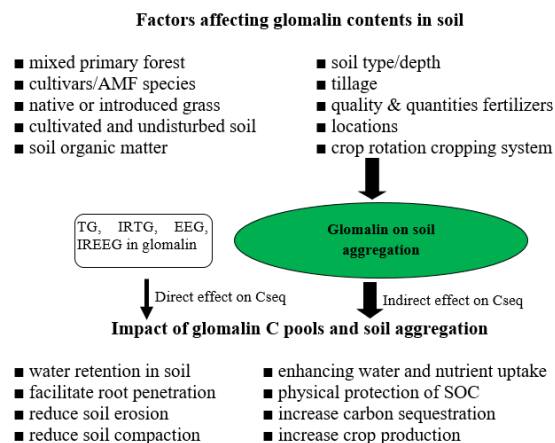


Figure 1. Factors affecting the glomalin and soil aggregation

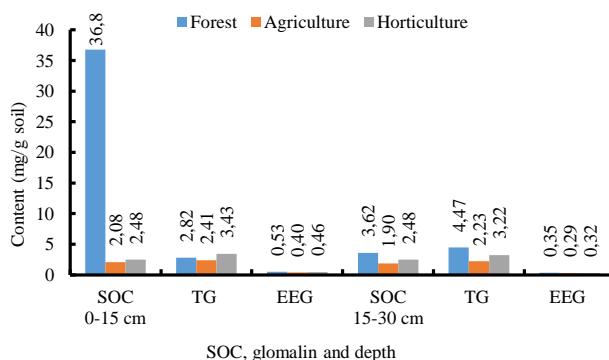


Figure 2. Soil organic carbon (SOC), total glomalin (TG) and easily extractable glomalin (EEG) in two soil depths of the three land use types (adapted from Nautiyal et al., 2019)

The AMF biomass decreased with the increase of soil depth under soybean-soybean rotation, and it increased more than 50% biomass at below 35 cm soil depth (Higo et al., 2013). Japanese winter wheat cultivars produce significant amount of extra radical hyphal biomass due to the penetration more than one meter of the soil depth

(Araki and Iijima, 2001). In respect glomalin amount, the correlation between soil and *in vitro* culture was negatively correlated due to the difference of hyphal length under fertile, non-fertile soils, and soil aggregates (Rillig and Steinberg, 2002; Lovelock et al., 2004). More carbon can store in 1 m depth to help carbon sequestration in soil. The content of SOC and the aggregate stability also impacted on the glomalin concentration in arable soils because it significantly functioned on SOM content, biological activity, and nutrient cycling in the soil (Wang et al., 2018; Bedini et al., 2009; Curaqueo et al., 2010; Sharif et al., 2018). Land use systems such as cultivation and fallow practices decreased the glomalin content in soil due to land use practices hampered the growth of AMF. The AMF biomass such as spores, extra radical hyphae, and

colonized root segments is contributed to the cropping system performance. The GRSP is a glycoprotein produced by the hyphae of AMF that contains large contents of metal ions (Wright et al., 1996). The AMF mediated glycoproteins contain significant amount of metal ions (Wright et al., 1996). Glomalin content results are presented in the Table 1, and the extent is 0.007 - 13.50 mg per gram soil in the different environments. The highest glomalin content was found in tropical rainforest (13.50 mg g<sup>-1</sup>), and the lowest glomalin content was observed in desert soil in the world. Glomalin can sequester 0.24 Mg C ha<sup>-1</sup> in soil when present at 1.10±0.04 mg g<sup>-1</sup> (Wang et al., 2018). It is estimated that AMF contributes 0.24 Mg C ha<sup>-1</sup> when glomalin content is 1.10±0.04 mg g<sup>-1</sup> soil (Wang et al., 2018).

Table 1. Glomalin in various environment

Environment	Glomalin	References
Agricultural land	0.3 – 0.7 mg g <sup>-1</sup>	Wright and Anderson, 2000; Wuest et al., 2005
Boreal forest	1.10 mg g <sup>-1</sup>	Treseder et al., 2004
Desert	0.003 – 0.13 mg g <sup>-1</sup>	Rillig et al., 2003; Treseder and Turner, 2007
Temperate forest	0.60 – 5.80 mg g <sup>-1</sup>	Steinberg and Rillig, 2003; Nicholas and Wright, 2005 Treseder and Turner, 2007
Temperate grassland	0.23 – 2.50 mg g <sup>-1</sup>	Lutgen et al., 2003; Batten et al., 2005; Nicholas and Wright, 2005
Tropical rainforest	2.60 – 13.50 mg g <sup>-1</sup>	Lovelock et al., 2004; Treseder and Turner, 2007
Antarctic region	0.007 – 0.15 mg g <sup>-1</sup>	Pohanka and Vleck, 2018
Marine sediments (0-10 cm) (Yellow river delta)	1.10 ± 0.04 mg g <sup>-1</sup> (0.24 Mg C ha <sup>-1</sup> )	Wang et al., 2018
Planted pine forest, secondary mixed pine and broadleaf forest	2.63±0.37, 4.22±0.31 and 4.99±0.57 mg g <sup>-1</sup> , respectively	Zhang et al., 2016
Tropical soil	60 mg cm <sup>-3</sup>	Rillig et al., 2001
Hawain soils	>100 mg g <sup>-1</sup>	Rillig et al., 2001
Arid soil	<1 mg g <sup>-1</sup>	Rillig et al., 2001
Prairie soil	28-45% C	Huang et al., 2011

#### **Effects of Glomalin on Soil Aggregate Formation**

Soil aggregates are composed of primary particles, which are strongly attached to each other in soil aggregation. Primary particles and clay microstructure, decomposable organic matter, fungal hyphae, and plant debris, small roots, and glomalin are the important components of soil aggregates. According to the concept I, larger micro-aggregates are formed with the combination of soil particles, fungal, and plant debris such as organic matter and so on. Micro-aggregates turn into macro-aggregates (> 250 µm in diameter) through the binding agents of decomposable organic materials and small diameter roots and associated AMF hyphae (Miller and Jastrow, 2000; Rillig and Mummey, 2006) (Figure 3). Hoorman et al. (2011) explained that three steps are followed for the formation of soil aggregation by the hyphal of AMF. The physical process is helped to form macro –aggregates with the combination of Hyphae of AMF and the soil particles. Second, in micro-aggregates of soil, fungi physically protect the clay and organic particles of before said micro-aggregates. Third, glomalin is produced by the plant root and fungal hyphae, which helped to combine glues micro-aggregates, and smaller macro-aggregates together turn into larger macro-aggregates. In concept II, recent research findings revealed that AMF hyphal containing glycoprotein act glue to bind

dispersed soil particles and other materials such as organic debris of the soil (Figure 3). Soil aggregation conducts the physical protection of SOC within aggregates to inhibit the microbial activity on SOC in soil (Amado et al., 2006). Further degradation of soil aggregation, it stores and protects the additional organic carbon in the soil. An amount of glomalin and the aggregate stability are closely correlated to the indirect effect of SOC storage in the soil (Wright et al., 2000; Rillig et al., 2001; Rillig, 2004; Wright and Nichols, 2002). Stable soil aggregates increased the storage of SOC by the inhibition of microbial activity (Rillig, 2004; Rillig et al., 2007). The IREEG pool is an important factor for soil aggregate stability irrespective of soil types and locations. IREEG is similar to glomalin in AMF hyphae through the use of analytical procedures (Wright and Upadhyaya, 1998). Filamentous structures of AMF mediated hyphae helped to stabilize the aggregation of soil. The AMF is responsible for the formation of macro-aggregates of soils is well documented by the different researchers (Wright and Anderson, 2000; Rillig et al., 2002). Glomalin abundant in soils also closely correlated with aggregate water-stability. Glomalin contributes an insignificant amount of carbon compared to the terrestrial carbon pool, but the glomalin mediated soil aggregation protects from the degradation of carbonaceous compounds inside the aggregates.

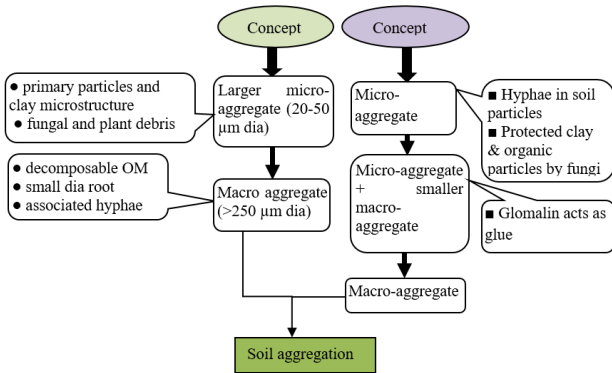


Figure 3. Concept of soil aggregation process by glomalin of AMF

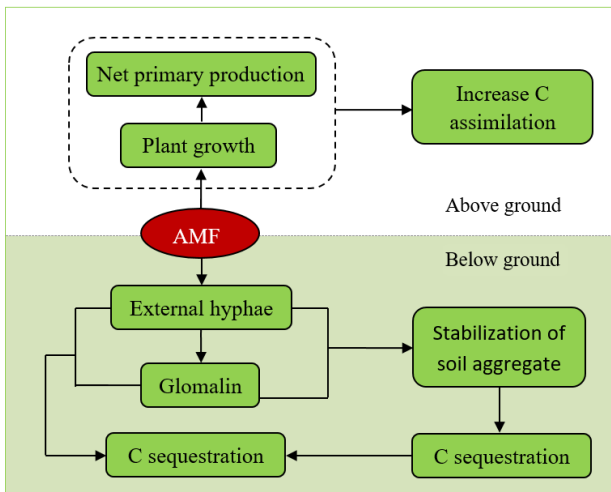


Figure 4. Regulation of carbon fluxes between biosphere and atmosphere by AMF (adapted from Zhu and Miller, 2003)

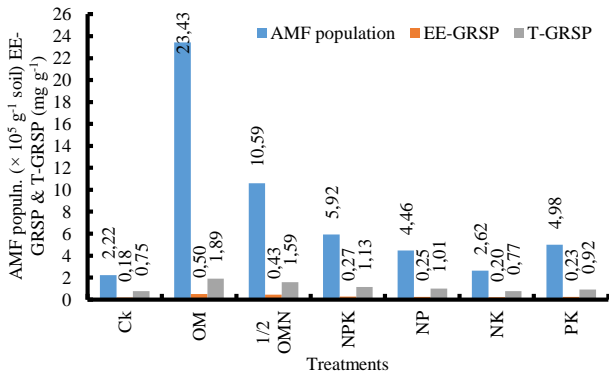


Figure 5. Effect of different fertilizer practices on AMF population and glomalin proteins

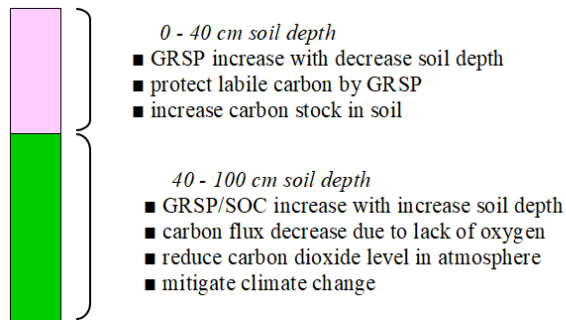


Figure 6. Impact of glomalin on different depths of soil

A sticky net is produced by AMF mediated hyphae and glomalin that pitfalls primary soil particles such as sand, silt, clay, and organic matter in the soil. Hyphae and glomalin together form a sticky net that traps particles of sand, silt, clay, organic matter and holds them together to create a lump or aggregate of the soil.

### Effect of Soil Aggregates on Carbon Sequestration and Crop Production

Labile carbon is protected in glomalin mediated soil aggregates (Liu et al., 2020). The GRSP variations in respect of the ratio of SOC, total nutrients, and TG display different depths of soil. The GRSP contributes significant amount of organic carbon storage and nutrient levels in deeper soil than surface soil in respect of GRSP/SOC ration. Curaqueo et al. (2010) reported that the significant relationship happened between GRSP and water stable aggregate in the soil. Conservation practice such as minimum tillage improved the significant AMF hyphal length, glomalin related soil protein, and water stable aggregates over traditional tillage practice (Curaqueo et al., 2010). No or minimum tillage increases of 44% total organic carbon in soil compared to conventional tillage. Micro-aggregates contain old organic carbon, and younger organic carbon stays in micr-aggregates in soil. Carbon sequestration efficiency is higher in upland soils than in paddy soils irrespective of all aggregates sizes in the same climatic condition and from the same parent material. The SOC ranges from 89.40 to 95.10% in different physical fractionations of soil. The amount of CO<sub>2</sub> levels depends on aggregate size, water stable aggregates, and glomalin under sandstone and serpentine media (Wright et al., 2000). Ambient and enriched CO<sub>2</sub> levels in serpentine increased the glomalin content compared to sandstone with ambient and enriched CO<sub>2</sub> levels. The WSA improved in sandstone with ambient and enriched CO<sub>2</sub> level compared to serpentine with ambient and enriched CO<sub>2</sub> level. This finding is concluded that the significant amount of aggregates improves water stable aggregates in sandstone. The AMF and plant roots symbiosis promote the absorption of nutrients and water to plants in different ecosystems (Figure 4). The AMF improves soil physical properties that can progress the aggregation of soil. Keeling et al. (1995) discussed that efforts should explore to sequester ever increasing CO<sub>2</sub> in terrestrial ecosystems. Green parts of the plant apprehend CO<sub>2</sub> from the atmosphere and redistribute the plant mediated photosynthate to roots and into the soil through root exudates (Rogers et al., 1994). Enrichment of atmospheric CO<sub>2</sub> increases glomalin production due to improves the symbiosis between glomalin mediated AMF and plant roots. At elevated CO<sub>2</sub> (700 μmol mol<sup>-1</sup>) level, EEG and TG increased 2.76 and 5.67% SOC in the surface soil layer over ambient CO<sub>2</sub> level in heavy metal contaminated soil. The GRSP also improves the rhizosphere SOC under elevated CO<sub>2</sub> level and heavy metal contaminated soil. Pools of glomalin such as easily extractable and TG related protein increase in elevated CO<sub>2</sub> level under improved symbiosis between AMF and *Robinia pseudoacacia* seedlings (Vodnik et al., 2008). Dai et al. (2013) reported that organic manure and mineral fertilizers and their different combinations produced the highest AMF population, EE-GRSP and TG-GRSP over control

treatment under winter wheat, and summer maize rotation (Figure 5). Kalam et al. (2011) reported that the maximum grain yield of rice ( $4.45 \text{ t ha}^{-1}$ ) was observed in  $\text{N}_{200}\text{P}_{40}$  + vesicular arbuscular mycorrhiza (VAM), which was statistically similar to  $\text{N}_{200}\text{P}_{20}$  + VAM treatment. Plant biomass and photosynthesis product allocation control the amount of glomalin production in soil. Plant gets sufficient amount of available nutrients by AMF symbiosis process in nutrient deficient soil. Photosynthetically plants supply carbon to AMF, which controls glomalin production by AMF (Treseder and Allen, 2000). The application of VAM inoculum may be stimulated growth and yield of rice as compared to un-inoculated rice plant. Maximum GRSP content was found in surface soil, but the maximum GRSP/SOC content was observed in 40-100 cm soil depth (Figure 6).

## Conclusion

The AMF mediated process involved in the storage of C in soils is the transfer of photosynthate from host plants to AMF hyphae. Effective AMF was identified for increasing glomalin concentration in soil. The highest GRSP content was recorded in surface soil, but the maximum GRSP/SOC content was observed in 40-100 cm soil depth. Glomalin is a carbohydrate associated glycoprotein and contains 30–40% (w/w) C which is assumed stable, and persistent in soil, and is thought to be produced in copious quantities by AMF. The results of this review revealed that glomalin improves soil quality as well as help mitigating the global climate change.

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