Review

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Beneficial services of Glomalin and Arbuscular Mycorrhizal fungi in degraded soils in Brazil

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ABSTRACT: Reducing soil degradation and its impacts on the environment have been one of the main challenges of the 21st century, exacerbated by a direct link between increases in the human population and soil degradation that raises current and future food security concerns. Despite this, experiences worldwide reveal that degraded land restoration projects have either achieved little success or failed. Thus, understanding the underlying causes and devising appropriate restoration mechanisms is crucial. Soil amelioration using beneficial microorganisms, particularly arbuscular mycorrhizal fungi (AMF), is essential and pragmatic. Glomalin, a type of glycoprotein produced by arbuscular mycorrhizal fungi in the phylum *Glomeromycota*, contributes to the mitigation of soil degradation. Moreover, AMF and glomalin are highly correlated with other soil physico-chemical parameters and are sensitive to changes in the environment. As a result of this, they have been recommended for monitoring the recovery of degraded soil or stages of soil degradation. In this review, we discuss the role of AMF and glomalin in the restoration of degraded soils, including improvements to the soil structure and soil organic matter (SOM), microbial activity, reduction of fertility loss, bioremediation, and mitigation of the effects of drought and saline stress. We highlight the research gaps and discuss the prospects. This knowledge will improve our understanding of the ecological conduct of glomalin and AMF, stimulate future research, and be useful to sustainable restoration of degraded lands. Furthermore, we discussed the challenges and obstacles in the legislation and future perspectives on the production of inoculants based on AMF in Brazil.
Keywords: tropical soils, recovery, bibliometrics, environmental security, soil health

Introduction

Globally, reducing soil degradation and its impacts on the environment has been one of the main challenges of the 21st century. Approximately 25 % of the world's soil is severely degraded, and 50 % is moderately degraded due to the aforementioned anthropogenic activities over the last few decades (Srivastava et al., 2019). Currently, Brazil is the second largest global supplier of food and agricultural products, and the country is poised to take the leadership in response to additional global demand (FAO, 2015). However, the agricultural expansion for the production of commodities is leading to severe erosion of arable land, nutrient loss, some overgrazing, environmental problems, and loss of biodiversity. According to predictions for the period 2015 to 2070, Brazil will be substantially affected by soil erosion processes (Borrelli et al., 2020). Moreover, the manifold risks created by pollution, landslides, drought, and pandemics (e.g., COVID-19 in which recovery rates hypothetically correlate with healthy diet and thus soil quality, since soils with optimal nutrients, water and air produce healthy crops) are aggravated by a skyrocketing human population, lifestyle changes, and inappropriate use of technology (Landrigan et al., 2018).

Given this scenario, soil restoration has become a cause of concern for global leaders and has been an important theme of global environmental policies (Jacobs et al., 2015). In 2015, the UN concretized these global commitments by adopting the 2030 Sustainable Development Goals with one of the 17 targets (Target 15.3) dealing with soil restoration (UN, 2015). According to specialists, Brazil could meet that goal well before the year 2030, if the right strategies associated with the political effort are put into practice (CGEE, 2016). Herein, we propose inoculation with beneficial soil microbes such as AMF, which, when associated with glomalin, can provide a better restoration outcome for degraded lands.

In this review, we highlight and discuss aspects related to the beneficial services of AMF and glomalin in degraded soils, the mechanisms used by the inoculants of these fungi and glomalin in the recovery process of degraded areas, the challenges of the production of mycorrhizal inoculants in Brazil, as well as the use of these microbiological attributes as indicators of soil quality. The monitoring of AMF and glomalin in the soil is of fundamental importance to identifying the stage of soil degradation/recovery.

Brief history of arbuscular mycorrhizal fungi and glomalin

Arbuscular mycorrhizal fungi

Arbuscular mycorrhizal fungi (AMF) is considered the oldest and most widespread type of mycorrhiza (Smith and Read, 2010). There are AMF fossil records dating back to the Ordovician period, 460 million years ago (Redecker, 2000). These fossils suggest that they may have played a key role in the colonization of land by plants during that time (Remy et al., 1994). Therefore, they were crucial to the adapting the land plants to biotic and abiotic conditions and thus favor survival, growth, and development.

Mycorrhizal associations can be found in approximately 95 % of all plant families and in 90 % of agricultural plants (Smith and Read, 2010). AMF is classified as a member of the Mucoromyceta subkingdom and the phylum *Glomeromycota* phylum including three classes (*Glomeromycetes*, *Archaeosporomycetes*, and *Paraglomeromycetes*) (Tedersoo et al., 2018) (Figure 1). AMF belongs to 11 families, 25 genera, and nearly 300 species (Spatafora et al., 2016; Schüβler and Walker, 2019). The vast majority of members of the phylum *Glomeromycota* fungi are obligate symbionts, that is, they depend on the carbon substrates provided by their host plants to survive (Siddiqui and Pichtel, 2008). In return, the fungi improve the supply of water and nutrients, such as phosphate and nitrogen to the host plant through extraradical and intraradical hyphae, arbuscules, and the root apoplast interface (Parniske, 2008). Mycorrhizal symbiosis is elemental to plant productivity and diversity and it is rare to find a situation in which AMFs are not of significant ecological importance. Its beneficial effects on plant nutrition and growth, as well as on the relief of biotic and abiotic stress, have been widely described (Souza et al., 2017; Diagne et al., 2020; Li et al., 2020; Singh et al., 2020).

Glomalin-related soil protein

The first discoveries of the glomalin protein refer to studies with antibodies in AMF initiated by Dr. Sara Wright (USDA-ARS, Beltsville, EUA), in 1987 (Purin and Klauberg Filho, 2010). Wright et al. (1996) motivated by taxonomic difficulties in identifying AMF, developed a specific antibody where AMF species showed reactivity, called MAb 32b11. Subsequently, it was demonstrated

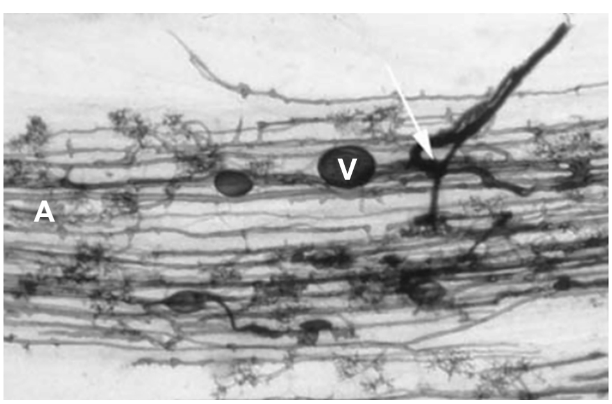

Figure 1 – Part of a colony of an AM fungus (*Glomus* sp.) with hyphae, arbuscules (A) and vesicles (V) growing from an entry point (arrow). Source: https://mycorrhizas.info/.

that the MAb 32b11 antigen in the mycelium of the fungus had a protein nature based on certain evidence: it was a protein proven by the Bradford method (Bradford, 1976) and had a positive result for binding lectin and its identification by capillary electrophoresis (Purin and Klauberg Filho, 2010). Wright et al. (1996) called this glycoprotein glomalin in reference to the *Glomales* taxon, to which the AMF belonged at the time. Another method of quantifying glomalin is through an immunological technique called ELISA. In this method, a monoclonal antibody MAb32b11 is used, produced from the spore macerate of *Glomus intraradices* injected into mice, recognizing the glomalin epitope only in AMF, and not reacting with other soil fungi (Wright et al., 1996). However, to quantify the content of this protein, the most used method (Silva Filho et al., 2018; Liu et al., 2020) is the Bradford colorimetric tests proposed by Wright et al. (1996) and Wright and Upadhyaya (1998).

Wright and Upadhyaya (1998) developed methods of extracting protein from the soil and introduced terms for the classification of glomalin based on these methods. It is considered that the ease of extraction of the fractions reflects the period of contact between the soil and the protein since the association of the protein with the organomineral surfaces increases with time (Koide and Peoples, 2013). The term "easily extractable glomalin" (EEG) refers to the most recent fraction deposited in the soil, whose extraction is done with 20 mM sodium citrate buffer and pH 7.0 in a short autoclaving cycle (30 min at 121 °C). In contrast, the term "total glomalin" (TG) designates the fraction most strongly fixed in soil particles, extracted with 50 mM sodium citrate and pH 8.0 in successive autoclaving cycles (60 min at 121 °C). Rillig (2004) still made adaptations of the nomenclatures proposed by Wright and Upadhyaya (1998), maintaining the methods of extraction and quantification. The terms TG and EEG were renamed Bradford-reactive soil protein (BRSP) and Easily Extractable BRSP (EE-BRSP), respectively, based on the possibility of coextraction of other proteins and also mentioning the non-specificity of the Bradford assay for a single protein.

Afterwards, Koide and Peoples (2013) and Wu et al. (2014a) also proposed another nomenclature, divided the GRSP into two fractions, soil protein related to easily extractable glomalin (EE-GRSP) and glomalin-related soil protein difficult to extract (DE-GRSP). EE-GRSP is considered to be a newly synthesized and relatively more labile glomalin, while DE-GRSP is, comparatively, an older glomalin originated from EE-GRSP turnover, more difficult to extract and recalcitrant in soils. The total soil protein related to glomalin (T-GRSP) is the sum of EE-GRSP and DE-GRSP. A recent study (Staunton et al., 2020) refutes this hypothesis that the easily extractable fraction is more recent compared to the total fraction, also highlighting that for complex surfaces such as soils, it is difficult to separate the effects of fixation which depends on the time that makes extraction less efficient, protein breakdown and loss of biological or biochemical activity (Hung et al., 2015). On the other hand, Staunton et al. (2020) support the fact that GRSP is not just the source of arbuscular mycorrhizal fungi. Thus, glomalin is the protein product of the gene, i.e., the protein produced by AMF, present in the walls of hyphae and spores. Soil fractions also referred to as "glomalin" summarily so far, will be referred from that point to as "glomalin-related soil protein" (GRSP), as proposed by Rillig (2004).

Beneficial Services of AMFs and GRSP in degraded soils

Soil degradation through erosion, compaction, loss of biological activity, acidification, salinization, or other processes can reduce soil quality by changing the soil attributes, such as soil biodiversity (e.g. AMF), GRSP content, soil organic matter, nutrient status, organic and labile carbon content, texture, available water-holding capacity, structure, maximum rooting depth, and pH (a measure of the acidity or alkalinity). Degraded soils capture less carbon from the atmosphere, interfering with climate change. By way of contrast, when managed sustainably, soil can play an essential role in reducing climate change through carbon sequestration (Figure 2). These edaphic perturbations limit the establishment of vegetation and soil restoration. Since the re-establishment of vegetation is a pioneering step for successfully recovering degraded lands, abiotic and biotic assistance is often provided to alleviate these plant stresses. For instance, inoculation with beneficial soil microbes in the rhizosphere is considered a vital option for improving the establishment of plant communities and to accelerate restoration of degraded terrestrial ecosystems (Chaudhary et al., 2020) (Figure 2).

In this context, several studies indicate an improvement in the growth and productivity of plants

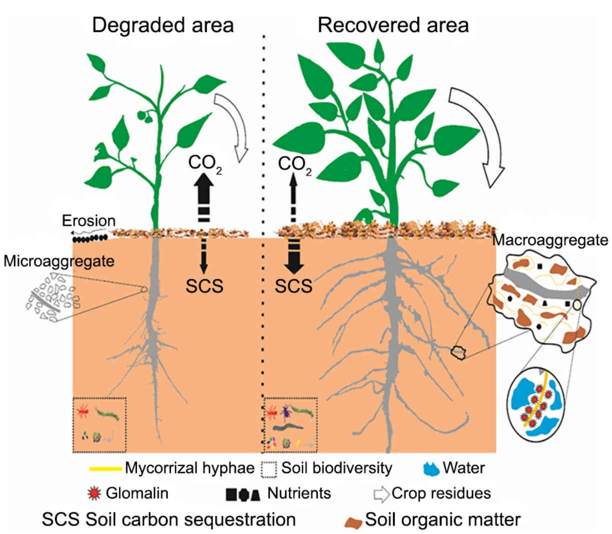

Figure 2 – Schematic representation of the main effects of AMFs and Glomalin on soil and plants.

inoculated with AMF in degraded soils under field conditions (Birhane et al., 2014; Lin et al., 2015; Manaut et al., 2015). Moreover, studies indicate that mycorrhization can induce 19 to 26 % more EE-GRSP and 13 to 20 % more T-GRSP in the mycorrhizosphere than in the non-mycorrhizosphere after inoculation with AMF (Wu et al., 2014b), implying that inoculation with AMF could help in the production of endogenous GRSP fractions for later use. Wang et al. (2015) found that the fraction of EE-GRSP was significantly higher, while the DE-GRSP and T-GRSP induced by mycorrhization were dependent on the AMF genotype since the hypha diameter, the hypha wall thickness, and its branching pattern collectively influenced the production of GRSP.

Improvement of soil structure

Soil disruption is one of the most important soil degradation indicators, mainly caused by the loss of soil organic matter (SOM), through intensive soil management practices and land-use changes (Wunder and Bodle, 2019). An essential service of AM fungi in natural as well as in degraded soils is the beneficial alteration of soil structure (Lehmann et al., 2017). AMF improves the soil structure both physically and chemically. Physically, soil particles are interconnected to each other through hyphae of arbuscular mycorrhizal fungi, promoting the stabilization of soil aggregates and increasing the absorption of soil nutrients by plants (Lehmann et al., 2017). Chemically, AMF releases glomalin, due to its stability and hydrophobicity, and works as an organic binder, helping to restore particulate material in the soil and promote the formation and improvement in the stability of aggregates (Rillig et al., 2017).

Strong positive correlation between GRSP and soil aggregate variables (R^2 = 0.41 – 0.78; $p < 0.05$) has been found in diverse soil types and climatic conditions (Wright and Upadhyaya, 1998; Luna et al., 2016; Liu et al., 2020). It has been suggested that GRSP enhances soil aggregate stability by improving the aggregate bond energy, particularly for macroaggregates (Ji et al., 2019). Moreover, an increase in the GRSP concentration in soil improved other soil physical properties, such as decreased bulk density and an increase in soil porosity, moisture content, and water-holding capacity (Gispert et al., 2013; Singh et al., 2016). Nobre et al. (2015) in a study on aggregation, GRSP and SOC in Chapada do Araripe (Ceará), found positive correlation between the carbon levels (TOC and POC), the GRSP fractions (EE-GRSP and GRSP) and between GRSP and aggregate stability, showing that the protein produced by AMF directly influences carbon concentrations and the stability of aggregates in the Chapada do Araripe soil. A similar result was found by Silva Filho et al. (2018), who found positive correlation between GRSP fractions and aggregate stability. In addition to this direct effect on soil structure, GRSP reduces soil erosion and improves soil thickness by forming soil aggregates (Gispert et al., 2013).

Improvement of soil organic matter (SOM)

The restoration of degraded lands also increases the soil organic matter (SOM), which is widely accepted as a solution to multiple soil degradation problems and global climate change (Singh et al., 2019). For instance, "4 per 1000 Initiative: Soils for Food Security and Climate" was launched at COP21, with a global aspirational goal to increase SOC stock at an annual rate of 0.4 % per year in soils of all anthropogenic and natural land uses (Soussana et al., 2019).

Total GRSP concentrations in soil certainly have a close link to total SOM concentrations (Li et al., 2020). Recent studies have shown that GRSP was the most important source of C in SOM-C (SOC) (Single et al., 2017; Whang et al., 2018; Zhang et al., 2017; Kumar et al., 2018). It has been estimated that GRSP contains approximately 37 % C and is responsible for 4-5 % of the total soil C (Rillig et al., 2001). The chemical structure of GRSP was revealed by the solid-state ^{13}C cross polarization magic angle spinning method (Zhang et al., 2017). The authors, found a higher proportion of aromatic C (~30 % of the total content) and carboxyl C (~40 % of total content), alkyl C (~30 %) and O-alkyl C (~50 %), and, further, calculated the recalcitrance index ((alkyl C + aromatic C)/(O-alkyl C + carboxyl C)), and found a significantly higher recalcitrance index for GRSP (mean range 73-102 %) versus total SOC (mean range 43-61 %).

The persistence of GRSP in the soil is estimated between 6 and 42 years in tropical soils, greater than that observed for mycelium, which is estimated to be a few days (Rillig et al., 2001). Steinberg and Rillig (2003), evaluating percentages of decomposition, found that the concentrations of GRSP decreased by 25 % in 150 days, while the mycelium of the AMF decreased by 60 %. Recent findings indicate that the greater contribution of GRSP to SOC in deep soils is related to the greater stability of SOC (Whang et al., 2018). Underground SOM is enriched with C compounds derived from microorganisms and can be depleted in energy-rich plant material compared to the top layer of SOM (Rillig et al., 2001; Rillig et al., 2003). Consequently, the increased fraction of C derived from GRSP for SOC with increasing sampling depth could provide new evidence that C derived from microbial biomass ,especially that of C-AMF, promoted the accumulation of SOC in the subsoil. Therefore, actively improving the GRSP content in the soil can be a strategy to improve the storage of C, and consequently, SOM in the soil. Currently, the viable alternative is to promote the growth of AMF that will subsequently produce glomalin in situ, as there is no other known source/mechanism of glomalin production (Singh et al., 2020).

Improvement in soil fertility

Depletion of soil nutrients is one of the main indicators of soil degradation, usually attributable to accelerated conventional cultivation practices to meet the demand for food and other agricultural products, but can also be caused by the lack of soil fertility management in pastures.

Several studies on GRSP have provided important data on its role to cope with this soil degradation problem (Singh et al., 2016; Wang et al., 2018; Zhang et al., 2017). The microbial decomposition of GRSP releases a range of nutrients such as carbon (30-40 %), nitrogen (3-5 %), phosphorus (3-4 %), iron (1-9 %) and other nutrients (1-2 %) (S, K, Ca, Mg, Zn, and Cu) in the soil for plant uptake (Singh et al., 2016; Wang et al., 2018; Zhang et al., 2017). A number of studies have shown the direct effects of increasing GRSP concentration on plant growth (Garcia et al., 2019; Muchane et al., 2018). Moreover, glomalin can indirectly enhance plant growth through improvements in AMF activity in the soil (Singh et al., 2020). Many studies have shown that inoculation of AMF heavily increased the concentration of rhizosphere GRSP (Xie et al., 2013; Yang et al., 2017; He et al., 2020). Furthermore, the effect of AMF on increased absorption and reduced leaching of nutrients has also been documented (Cavagnaro et al., 2015; Querejeta, 2017).

AMF plays a crucial role in tropical soils, especially in regard to supporting the phosphorus absorption process, since in these soils the phosphorus loss is high due to the fixation process (Fontes and Alleoni, 2006). Through extensive networks of extraradical mycelium, AMF accesses soil mineral nutrients inaccessible to their host plant, including nutrient pools beyond the root depletion zone (Smith and Read, 2010), and may also mineralize organic P sources (Koide and Kabir, 2000). Mycorrhizal symbiosis can also increase the absorption of N and its immobilization in fungal biomass, significantly reducing the loss of this nutrient in agricultural or natural ecosystems (Cavagnaro et al., 2015). Such absorption and immobilization, especially of ammonium, reduces nitrification and, consequently, loss by leaching, since nitrate is extremely mobile in the soil. In addition, there is a reduction in the production of nitrous oxide (Storer et al., 2018), a greenhouse gas capable of promoting heating approximately 300 times higher than that of CO_2 (IPCC, 2001). It is important to note that the effect of AMF as a soil conditioner has been well documented. However, there is still a gap in the research on the role of glomalin in increasing nutrients, and also as prebiotics for plants. Further studies should be conducted in this area to fill in this gap in the research.

Improvement in microbial activity

The positive correlation between GRSP and microbial activity has been documented in previous studies. Since AMF is a major producer of glomalin, a higher GRSP level in the soil indicates higher soil mycorrhizal fungal activity. Therefore, GRSP is an indicator of higher microbial activity since AMF body parts (extraradical hyphae and spores) constitute 20-30 % of soil microbial biomass, and the contribution of AMF in total soil microbial respiration is substantial (up to 25 %) (Zhang et al., 2016). Moreover, positive correlation between GRSP and microbial biomass C and microbial respiration has been found in multiple soil environments (Gispert et al., 2013; Wang et al., 2018). GRSP can also increase microbial catabolic functions (i.e., the release of extracellular enzymes) as it is a microbial decomposition substrate (Singh et al., 2020). Soil extracellular enzyme activities, such as b-glucosidase, phosphatase, fluorescence diacetate, and dehydrogenase, showed positive correlation with the GRSP (Wu et al., 2015). For example, in a microcosm experiment, Wu et al. (2015) found increasing GRSP concentration increases b-glucosidase, catalase, peroxidase, and phosphatase enzyme activities in soil. Similarly, in a free-air CO_2 enrichment experiment with tree saplings (*Tectona grandis* and *Butea monosperma*), Singh et al. (2019) reported positive correlation between GRSP and acid phosphatase, b-glucosidase, dehydrogenase, and fluorescein diacetate enzyme activities.

Bioremediation

Soil degradation problems are not only linked to agriculture intensification and over-exploitation of nutrients (e.g., carbon, nitrogen, and phosphorus) of soil but are also caused by multiple pollutants (e.g., heavy metals, polycyclic aromatic hydrocarbons, nanomaterials, etc.) from various anthropogenic source discharge on land (Wu et al., 2020). The AMF plays a crucial role in areas degraded or polluted by heavy metals, helping plants survive in such stressful conditions (Hildebrandt et al., 2007; Conversa et al., 2019; Song et al., 2020). The mechanism used by AMF to promote heavy metal remediation can be activated through hyphal "metal binding", which reduces the bioavailability of elements, such as Cu, Pb, Co, Cd, and Zn (Audet and Charest, 2007). They also expressed certain metal transporters that could be involved in heavy metal tolerance in plants inoculated by AMF (Diagne et al., 2020). For instance, Zn transporters, such as GintZnT1 from *R. irregularis* (González-Guerrero et al., 2016). Several putative gene codings for Cu, Fe, and Zn transporters were identified in AMF (Tamayo et al., 2014).

Glomalins also play a key role as active agents in providing tolerance to heavy metals. According to Purin and Rillig (2007), one of the functions of glomalin in AMF is complex protein-metal formation. The findings suggest that the glomalin proteins' assistance in wall binding has additional functions other than that of cytoplasmic heat shock proteins, which further influence the AMF and plants to withstand metal stress. Studies conducted by Chern et al. (2007) revealed the contribution of GRSP in decrementing the phytotoxicity induced by Cd, Cu, and Zn. In soils contaminated with heavy metals, Gonzalez-Chavez et al. (2004) found that the GRSP proteins can quench up to 80 mg of Cd, of Pb, and 4300 mg kg^{-1} of Cu.

Aluminium (Al) toxicity is the main factor limiting plant growth in acid soils that are widely distributed throughout tropical and subtropical regions (Sade et al., 2016). Management of arbuscular mycorrhizal fungi (AMF) is considered an important factor in the enhancement of tolerance to potentially toxic elements such as Al (Seguel et al., 2017; Cornejo et al., 2017). A number of studies have revealed several possible mechanisms of Al tolerance induced by AM fungi in higher plants, including that (a) AM fungi improve the uptake of phosphorus (P) and other nutrients in their host plants through Al-P interaction in colonized roots, which is critical to the maintainance of plant growth under Al stress (Seguel et al., 2013); (b) AM fungi stimulate the processing of carbon in roots through the citric acid cycle to enhance the exudation of organic acids, which chelates Al^{3+} in the rhizosphere (Seguel et al., 2013); (c) GRSP produced by AM fungi has the capacity to sequester Al^{3+} in the rhizosphere (Seguel et al., 2013); (d) AM fungal structures such as spores and hyphae have the capacity to bind Al directly or build an enlarged mycorrhizosphere in which Al is detoxified (Joner et al., 2000; Göhre and Paszkowski, 2006). According to Aguilera et al. (2018), AMF has the potential to alleviate Al phytotoxicity through a chemical barrier in which glomalin sequesters Al beyond the root surface, which seems to be an important trait of AMF and would be used for developing management strategies of acidic soils with high Al levels.

Reducing the effects of drought and saline stress

Drought and salinity are severe and extensive soil stressors, intensified by climatic change, that produce land degradation, whose negative effects on plant growth may be mitigated by the action of AMF and GRSP (Elhindi et al., 2017; Chi et al., 2018; Ji et al., 2019). There are different mechanisms through which AMFs reduce the adverse effects of abiotic stresses. Among these mechanisms are increased water use efficiency, improved stomatal conductance and increased activity of antioxidant enzymes to reduce peroxidative damage (Duc et al., 2018; Li et al., 2019). Moreover, under osmotic stress, aquaporins (AQPs) are important in regulating the water flow of plants. Aroca et al. (2009) cloned the first aquaporin from an AMF (GintAQP1). They found that GintAQP1 expression was upregulated in parts of the mycelium that were not osmotically stressed by NaCl while other parts of the mycelium were stressed. This suggests a possible communication between the non-stressed and the stressed mycelium. Two functional genes have been characterized, GintAQPF1 and GintAQPF2, which code for AQPs present in the AMF *Rhizophagus intraradices* (Li et al., 2013a), that are overexpressed under osmotic stress conditions, helping the fungus to tolerate stress and potentially increasing the water supply to a host plant under these conditions (Li et al., 2013b).

AMF have been consistently shown to improve nutrient uptake and maintain ionic homeostasis in saline soils (Heikham et al., 2019). AMF reduces the translocation of Na^+ ions to plant tissues, preventing their concentration from reaching toxic levels. This is due to the ability to retain these ions in structures such as the intraradical mycelium and vesicles, by accumulating ions in their vacuoles (Mardukhi et al., 2011). Moreover, studies with *Rhizophagus intraradices* have shown their ability to selectively absorb mineral nutrients such as K^+, Mg^{2+} and Ca^{2+}, preventing the entry of Na^+ in the mycorrhizal structures, maintaining high ratios of K^+: Na^+, Ca^{2+}: Na^+ and Mg^{2+}: Na^+ (Mardukhi et al., 2011).

In addition, Garcia et al. (2019) showed that, in the presence of salinity, soil inoculated with AMF increases the content of GRSP, which has numerous beneficial effects on the restoration of soil health. Abiotic stresses, as drought and salinity, has been reported to increase GRSP contents (Hammer and Rillig, 2011; Krishnamoorthy et al., 2014; Zou et al., 2014; Garcia et al., 2019). A study carried out by Chi et al. (2018) showed that exogenously applied GRSP could strongly stimulate root morphology and plant growth under drought stress. GRSP can also modulate the phytohormones especially auxin (IAA), abscisic acid (ABA), and methyl jasmonate (MeJA) concentrations under drought stress. Therefore, the exogenous treatment of GRSPs is suggested as a plant growth regulator for improving drought tolerance (Chi et al., 2018). Wu et al. (2008) showed that inoculation with *Funneliformis mosseae* and *Diversispora versiformis* increased the production of GRSP under water deficit, by promoting the stability of soil aggregates. In this context, Nichols (2008) further proposed that GRSP can act as a coating on fungal hyphae to prevent water loss, and by the formation of a hydrophobic layer in the aggregate topsoil of the soil to reduce water loss in soil aggregates under drought stress. Later studies by Wang et al. (2015) showed the strong positive relation of exogenous EE-GRSP to soil aggregation, rhizospheric enzyme activities and plant growth. Ji et al. (2019) found that AMF and GRSP contribute to the formation and stability of soil water-stable macroaggregates even under drought stress conditions.

Advances and perspectives: production of AMF inoculants

Many studies have described the importance of inoculation of AMF for development in agriculture, as well as for reforestation programs in degraded areas (Birhane et al., 2014; Lin et al., 2015; Souza et al., 2017). However, obligate biotrophic hinders the production of arbuscular mycorrhizal inoculants since the fungus requires metabolically active roots to complete its life cycle (Moreira and Siqueira, 2006). Consequently, they cannot be multiplied separately in a defined culture medium (Douds Jr. et al., 2006). Because of this, it is very difficult to develop low-cost methods for high-quality inocula production on a large scale (IJdo et al., 2011). Thus, these fungi are usually multiplied in host plants in culture pots, aeroponic cultivation, hydroponics, or in vitro culture with genetically transformed roots (IJdo et al., 2011). These processes are carried out under controlled or semi-controlled conditions, such as greenhouses or growth chambers (IJdo et al., 2011).

The richness of AMF in the production of inoculants is considered to improve their effectiveness. The plant's response is substantially less when inoculated with unique species of AMF and the response increases when several species of fungi are used for soil inoculants (Hoeksema et al., 2010). Inoculation with AMF should be carried out whenever possible, in order to guarantee fast and efficient colonization. It is essential in situations where the presence of native AMF propagules is low or nonexistent or in communities with low diversity of AMF (Souza et al., 2017). It is important to highlight the potential negative consequences of introducing non-native soil organisms to restoration sites since these introductions may not be reversible. Commercially produced AMF inoculants represent a small genetic pool of fungi selected to be at once generalists and aggressive colonizers. These traits have the potential to threaten local AMF communities, which may not be resistant to alien introductions (Hart et al., 2017). Evidence has been accumulating indicating that non-native commercial fungi are not beneficial to restoration (Middleton et al., 2015; Koziol et al., 2018).

A number of authors suggest that as a recovery strategy for areas degraded by mining, AMF inoculation may be more suitable only under the few conditions where the native inoculum has disappeared or existed in small quantities (Brundrett and Abbott, 2002), and it would be better to focus on managing the local AMF community rather than inoculation (Koide and Mosse, 2004; Souza et al., 2017). Although inoculation may improve growth during the first few years, uninoculated plants may eventually become colonized by resident AMF (Estaún et al., 2003) and perform as good or better than inoculated plants (Middleton et al., 2015).

The production of aseptic inoculum has been achieved through in vitro cultivation of the fungus in association with root cultures transformed by *Agrobacterium rhizogenes*. Other production methods generally do not guarantee the production of inoculants free from other microorganisms, thus making it difficult to register arbuscular mycorrhizal inoculants in Brazil. Production in greenhouses, where fungus is cultivated with species of host plants, usually grasses, is a relatively cheap and efficient method, and is the most used by research institutions and universities in Brazil, beit for the production of inoculum or for maintaining crop collection (Souza et al., 2017).

Production of aeroponics systems has also been developed by Brazil's research institutions (Santana et al., 2014). Despite the high technological level developed in Brazilian research institutions, the national inoculant industry has not yet incorporated the technologies.

Despite the high technological level developed in Brazilian research institutions, the national inoculant industry has not yet incorporated the technologies. Certain products are obtained from the in vitro cultivation of the fungus associated with root crops. Nevertheless, in the majority of cases, inoculants produced in systems with plants are also commercialized, either in cultivation pots with different substrates or through more sophisticated techniques, such as hydroponics and aeroponics (Ijdo et al., 2011).

Another method that is gaining notoriety is the production of inoculum under field conditions, known as the on farm method (Douds Jr. et al., 2006). In this process, the soil collected in the farm is used as inoculum. The soil containing propagules of AMF is inoculated on a substrate based on vermiculite and an organic compound and is cultivated with grasses, such as corn, sorghum, and millet as well as legumes. Subsequently, after a period of four to six months, the substrate containing multiplied spores is used as an inoculum (Souza et al., 2017). This technique is a low-cost alternative for farmers; moreover, they can produce seedlings already mycorrhizal with this benefit enhancing the establishment of seedlings in the field.

In Brazil, present legislation for registering microbial inoculants for agriculture makes it challenging to produce and trade official products containing AMF. Given this scenario, changes to, and/or the creation of laws are necessary to expand the limited market for inoculants of AMFs currently in existence in Brazil (Saggin Júnior, 2019). These modifications will allow norms for inoculants and agronomic tests to be directed to AMFs and the presence of multiple species in the inoculants. In addition to allowing for the sale of soil conditioners that contain AMF propagules, taking into account the supply of AMF species that cannot be multiplied under axenic conditions AMFs remain important to forest production. Moreover, the proposed changes will facilitate the registering of AMF inoculants produced under axenic conditions, and are not subject to specific requirements for bacterial inoculants. Despite these challenges, in 2018 the first mycorrhizal inoculant was registered with the Ministry of Agriculture, Livestock and Supply (MAPA) for commercial use, and as an application for soybean and corn seed treatment (as well as for wheat, rice, barley, oats and beans).

Gomalin and AMF as soil indicators in degraded areas

Given the relevance of AMF and GRSP for the restoration of degraded soils, it is recommended that they are assessed in studies of anthropogenic impacts and monitoring programs (Islas et al., 2016; Silva et al., 2017; Pereira et al., 2018; Šarapatka et al., 2019). Since both AMF and GRSP have positive correlation with the main edaphic attributes used for soil quality assessments (Silva et al., 2017; Šarapatka et al., 2019); i.e., the greater the diversity of AMF species and the GRSP content, the better the soil quality (Silva et al., 2017; Pereira et al., 2018). Moreover, they are susceptible to land-use change (Silva Filho et al., 2018; Silva et al., 2016; Nogueira et al., 2016) and management practices (Islas et al., 2016).

Given the importance of GRSP as soil health components (Pereira et al., 2018; Silva Filho et al., 2018) research into this variable has been growing worldwide (Figure 3A and B). In Brazil, there was a peak in studies on this topic in 2012 and 2016, with a decrease in subsequent years. However, research associating GRSP, AMF, and restoration of degraded areas are scarce in Brazil (Figure 3C, D and Table 1), limited to the southeast and northeast regions, under the Atlantic Forest and Caatinga biomes (Table 1). Our bibliographic research reveals that there is a scarcity of studies on the topic in areas such as the Amazon and Cerrado biomes, for example, where a large part of the soils is at some level of degradation, either by intensive use of the soil, or by natural events such as forest fires. In addition, most research evaluates the behavior of AMF and GRSP under different techniques for recovering degraded areas (Table 1). There is little research on using inoculated species in degraded areas.

Final Remarks and Future Perspectives

Soil restoration is essential to providing food to people, strengthening and sustaining ecosystem services. The soil is non-renewable on a human timescale (decades), and sustainable alternatives of soil restoration such as the use of AMF and GRSP are vital to guaranteeing goods for future generations. Recognizing that this study addresses the benefits that AMFs associated with GRSP can improve soil quality in terms of soil structure, increase SOM, reduce fertility losses, and increase microbial activity thereby remedying soils contaminated by heavy metals. The adoption of these technologies to restore degraded soils is reflected in increases in production, which are so important to ensuring that they continue to provide their wide range of services for the soon to be 9.8 billion inhabitants of our planet. Moreover, they can assist in the mitigation of global warming through a potential increase in soil carbon sequestration.

Despite biotechnological advances related to the production of AMF in Brazil, production costs and bureaucracy established by MAPA have still been limiting factors on production in Brazil. It is therefore necessary that changes and/or the introduction of new laws to facilitate the commercialization of these products and enable the use of this technology for Brazil to be able to comply with international agreements (Paris Agreement) and achieve more ambitious goals such as the sustainable development objectives proposed in the Agenda for 2030. Brazil has a significant amount of degraded areas that, if they were recovered and incorporated into the production system, would eliminate the need to clear new land to support increased agricultural and livestock production.

Table 1 – List of studies evaluating the use of AMFs and glomalin as indicators for assessing the recovery of degraded areas in Brazil.

Year	Authors	Local	Biome	Study areas	Main results
2010	Mergulhão et al., 2010	Araripina-PE	Caatinga	-Native forest -Degraded area surrounding the mine -Waste deposit area -Interface between the waste deposit and mining degraded area	The EEG can be used as an indicator of differences between preserved "caatinga" versus areas impacted by gypsum mining.
2012	Carneiro et al., 2012	Gilbués-PI	Caatinga	-Area under recovery with plant legumes and forage grasses -Area degraded with erosion -Area with initial degradation process -Native forest	The cultivation of grasses and forage legumes associated with erosion control practices increases number of AMF community in degraded areas
2012	Silva et al., 2012	Campos dos Goytacazes-RJ	Atlantic Forest	-Pure planting of Eucalyptus camaldulensis -Pure planting of *Acacia mangium* -Consortium of Eucalyptus camaldulensis + Acacia mangium -Degraded area with vegetation spontaneous	-The diversity of AMF spores, T-GRSP and EE-GRSP increases with the revegetation of the clay pit; -Consortium of *Eucalyptus camaldulensis* + *Acacia mangium* promotes an increase in the diversity of AMF, in relation to eucalyptus monoculture.
2013	Vasconcellos et al., 2013	São Paulo	Atlantic Forest	-Native forest area (NT) -5 years after revegetation -10 years after revegetation -20 years after revegetation	-Higher diversity of AMF in NT than others; -AMF species richness was correlated with the gradient of environmental restoration; - EE-GRSP and T-GRSP positively related to total carbon, nitrogen and enzymatic activity, but negatively related to bulk density. -Glomalin and AMF may be used as indicators of soil quality in the Atlantic forest.
2014	Silva et al., 2014	Campos dos Goytacazes-RJ	Atlantic forest	-Soil degraded by clay extraction with spontaneous vegetation -Pure plantings of *Sesbania virgata* -Integrated system with *Eucalyptus camaldulensis* and *Acacia mangium*	The revegetation of the clay extraction pit with *Sesbania virgata*, in pure or intercropped plantations reduces the amount of soil protein related to glomalin
2015	Silva et al., 2015	Mataraca-PB	Atlantic Forest	-Natural and revegetated area	Revegetated areas areas had a higher species richness of AMF than Natural areas.
2016	Nogueira et al., 2016	Passa Vinte-MG	Atlantic Forest	-Secondary Forest -Natural Pasture -Natural Regeneration areas	The conversion of native forest into pasture reduced T-GRSP and EE-GRSP.
2017	Silva et al., 2017	Pinheiral-RJ	Atlantic Forest	-Secondary forest early stage -Secondary forest medium stage -Secondary forest advanced stage -Pasture -Perennial agriculture -Annual crops	The conversion of forest to agriculture reduces the soil protein content related to glomalin.
2018	Pereira et al., 2018	Contendas do Sincorá-BA	Caatinga	Three types of forest management -Clear-cutting -Selective logging based on diameter -Selective logging based on species -Control area (Native forest)	-The AMF community is sensitive to changes caused by forest management. -The different managements cause changes in the AMF community. -The AMF community can recover over time.
2018	Silva Filho et al., 2018	Sobral-CE	Caatinga	-Overgrazing -Exclusion -Native Forest	The contents of GRSPEE and GRSPT of the native forest were higher than those found in the areas of exclusion and overgrazing
2019	Silva et al., 2019	Assú-RN Pendências-RN Carnaubais-RN	Caatinga	-Gravel mine J1-P -Gravel mine J2-P -Umpjack base PB-P -Waste disposal area WDA-P -Native vegetation	AMF presented lower densities in the evaluated areas when compared to those in the adjacent native vegetation areas.
2020	Weber et al., 2020	Acaraú-CE	Atlantic Forest	-Forest planting with native tree species -control area (non-forested area)	The cultivation of these species for 6 years increases glomalin-related soil protein.

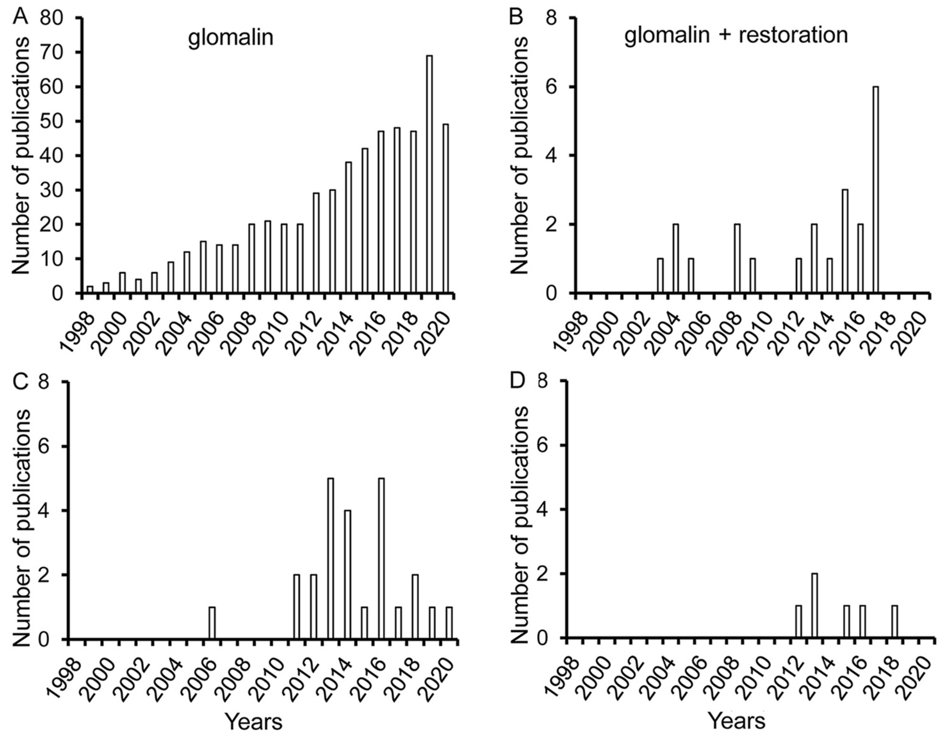

Figure 3 – Survey of the number of studies in the Web of Science database about glomalin and restoration of degraded areas in the world (A and B) and in Brazil (C and D).

Authors' Contributions

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