Prospects of Cropping with Polysaccharides Producing Microbes Under Drought Stress

Kuraklık Stresi Altında Polisakkarit Üreten Mikroorganizmalarla Ekim İmkânları

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ABSTRACT

Drought and water stress are the major abiotic stresses that limit plant growth. Plant growth-promoting rhizobacteria, well known for their growth-promoting attributes, produce extracellular polysaccharides that form rhizosheath around the roots, thereby protecting them from desiccation for a longer duration. Arbuscular mycorrhizae, one of the key determinants of soil quality, secrete glomalin protein, which shows soil aggregation properties and helps in increasing water stability, thereby overcoming drought conditions. Increasing extracellular polysaccharide-producing plant growth-promoting rhizobacteria and mycorrhizal fungi density in the rhizospheric soil can be a means to improve the survival of plants during water stress periods. The present review highlights the role of microbes producing extracellular polysaccharides in the maintenance of soil health and plant growth under drought.

Keywords: Drought stress, extracellular polysaccharides, glomalin, PGPR, AMF, microbes

ÖZ

Kuraklık/Su stresi, bitki büyümesini kısıtlayan önemli bir abiyotik strestir. Büyümeyi teşvik edici özellikleriyle iyi bilinen bitki büyümesini teşvik eden rizobakteriler (PGPR), köklerin etrafında kuraklık süresince onları daha uzun süre kuraklığa karşı koruyan hücre dışı polisakkaritler (EPS'ler) üretirler. Toprak kalitesinin temel belirleyicilerinden biri olan arbusküler mikorizalar, toprağın topaklanma özelliklerini gösteren ve su stabilitesinin arttırılmasına ve böylece kuraklık koşullarının aşılmasına yardımcı olan glomalin proteinini salgılar; bu protein, toprak agregasyon özelliklerini gösterir ve dolayısıyla kuraklık koşullarını aşarak su stabilitesini artırmaya yardımcı olur. Rhizosferik toprakta EPS üreten PGPR ve mikorizal mantar yoğunluğunu artırmak, bitkilerin su stresi dönemlerinde hayatta kalma şansını artırmak için bir yol olabilir. Bu derleme, EPS üreten mikroorganizmaların kuraklık altında toprak sağlığının ve bitki büyümesinin korunmasındaki rolünü vurgulamaktadır.

Anahtar Kelimeler: Kuraklık stresi, ekstrasellüler polisakkaritler, glomalin, PGPR, AMF, mikroorganizmalar

Introduction

Agriculture is the art of domesticating plants for food, fiber, biofuel, medicinal purposes, and other products used to sustain and improve human life. Agriculture in the past century has seen large rises in productivity due to innovative human ideas on mechanization, synthetic fertilizers, biofertilizers, pesticides, and selective breeding. However, the world populace is thriving quickly and is relied upon to achieve 10 billion by the year 2050. The increasing population has exerted serious pressure on the existing agricultural land, demanding intensified crop production. Abiotic stresses like soil sodification, soil salinization, soil pH, drought, and environmental temperature are adding further constraints. Abiotic stress straightforwardly damages the farmable area, affecting the crop yield. Of all the 20th century climate risks, water stress brought on the greatest negative impact, and decreased rainfall was the major climatic factor affecting crop growth.

The natural soil microbial assembly dwelling in the rhizosphere and on the surface of the plant roots, which execute beneficial effects on the overall welfare of the plants, is categorized as plant

growth-promoting rhizobacteria (PGPR). Generally, about 2–5% of rhizosphere bacteria are PGPR. Majority of credible groups of PGPR belong to genera belonging to *Agrobacterium, Acineto-bacter, Azotobacter, Arthobacter, Azospirillum, Burkholderia, Bradyrhizobium, Frankia, Serratia, Rhizobium, Thiobacillus, Pseu-domonas,* and *Bacillus.* Plant growth-promoting rhizobacteria have mostly been studied for their abilities to improve plant growth by direct mechanisms, like enhancing nutrient content and phytohormone, extracellular polysaccharide (EPS) production, or indirect mechanisms, like siderophore production and protecting plants against pathogen attack by HCN production (Hakim et al., 2021). Adopting PGPR's can be an effective strategy for cropping under drought stress, as the EPSs secreted by the rhizobacteria in the soil along with the adjacent mineral particles form a sheath around the plant roots, which protects them from desiccation under the declining water conditions (Prasad et al., 2022). Polysaccharide-producing PGPR have also been reported to help in maintaining high water content in the rhizosphere in sandy soils (Khan et al., 2017; Zheng et al., 2018). They also help in the formation of macroaggregates, which improve soil structure. Extracellular polysaccharides can have an imperative role in ecosystem management as they exhibit multifaceted roles like protection of plants from desiccation, microbial aggregation, plant–microbe interaction, surface attachment, and bioremediation, which can help in ecosystem establishment.

Arbuscular mycorrhizal fungi (AMF), the other microbial group forming symbiotic association with the roots of higher plants, have profound effects on host plant physiology, soil engineering, and ecological interactions. Arbuscular mycorrhizal fungi well recognized for nutrient mobilization in plants (Miller & Jastrow, 2000) also help in encountering drought by secreting glomalin protein which shows soil aggregation properties (Rillig, 2004) thereby improving soil water stability. Understanding control over glomalin production and its mechanism of production can help maximize the contributions of arbuscular mycorrhizal mycelium to soil aggregation and water stability. Arbuscular mycorrhizal fungi colonization increases host growth rates during droughts by increasing water use efficiency and affecting soil enzymatic activity, which increases nutrient acquisition. Understanding the rhizospheric microbiome and maintaining the density of EPS-producing microbes can be helpful in overcoming the water stress responses in plants.

Besides PGPR and AMF, several other EPS-producing bacteria, algae, fungi, and yeasts are much worked upon for their industrial exploitation and biofilm properties but less studied for their plant growth-promoting attributes. Extracellular polysaccharides are one of the principal components involved in the formation of the extracellular biofilm matrix, which protects microorganisms from the adversities of pH, temperature, antibiotics, host immune defenses, and so on. The past decade has witnessed an increase in exploring natural polymers in areas of chemistry, medicine, and the food industry. Because of their unique structure and composition, they have an inherent ability to increase holding water, which makes them widely used as viscous, stabilizing, and emulsifying agents in the food industry and to improve the rheological properties, texture, and sensibility of bread and fermented milk products such as yogurt and cheese. In addition, EPSs also have potential health benefits such as antioxidant, anticancer, anti-inflammatory, antiviral, and cholesterol-lowering effects (Nguyen et al., 2020). Among EPS-producing bacteria, lactic acid bacteria (LAB) have captured much attention from researchers due to

their strong ability to produce EPS. Introducing EPS-producing microbes in rhizosphere engineering can be helpful in improving plant growth, disease, and stress resistance by artificially reconstructing the plant-root microbiome and overcoming the barriers to intensive cropping under adversity.

Drought Response in Plants

Stress in general limits the growth of plants for some period of time until either the stress is removed or the plant is able to adjust its metabolism to overcome the stress. Soil drought often prompts an atmospheric drought, and if both combine, it becomes disastrous. Plants struggle more against soil drought than against atmospheric drought. A plant is stressed when there is a reduction in some physiological rate (water or nutrient absorption, photosynthesis, respiration, growth, development, reproduction, or others) below the maximum possible rate expressed under optimal conditions. Stress obstructs the plants from attaining genotypic potential, which severely affects productivity. In response to environmental stress, alterations in the levels of several compatible solutes like proline, sugar, polyamines, polyhydric alcohols, betaines, amino acids, and quaternary ammonium compounds are observed. Antioxidants are the principal defense system against oxidative damage in plants. These antioxidants, comprising superoxide dismutase, peroxidase, catalase, and many nonenzymatic compounds like carotenoids and ascorbate, get enhanced in response to water stress (Nadeem et al., 2021; Prasad and Raghuwanshi, 2022).

Water performs the main role of absorbing nutrients from the soil and transporting them to different parts of the plant. Morphologically, drought injury is evident as stunted growth, a decrease in the growth of the lateral root, and enhanced waxy deposition of epidermal and cortical cells, thereby decreasing intercellular space, which maximally affects growth, development, and plant productivity. Physiological characterization of plants subjected to drought reveals that the stress has several unique aspects, including high respiration with low photosynthesis, closed stomata, and high leaf temperature. Roots are the area where a plant first faces water stress and likely responds to stress conditions. Under limited water availability, the root–shoot ratio of plants increases because roots are less sensitive than shoots to growth inhibition by low water potential (Latif et al., 2022). Thus, to make plants drought-tolerant, better rhizo-engineering is always advisable. Microorganisms residing in the rhizosphere encode more genes than the host plants and form a stable community structure through collaboration and competition, which is crucial for growth, development, and resistance against adversities (Bai et al., 2022).

Bacterial Extracellular Polysaccharides

Extracellular polysaccharides can be referred to as those polysaccharides that are synthesized and then secreted in the external environment. Many times EPSs are synthesized extracellularly by the cell wall-anchored enzymes of bacteria and archaea. The term exopolysaccharide was proposed by Sutherland (Sutherland, 1977) for these EPS which is often used interchangeably. Extracellular polysaccharides is a heterogeneous mixture of polysaccharides, proteins, nucleic acids, and lipids in the form of long chain molecules, with a molecular weight of 10–30 kDa. Although bacteria synthesize only a few intracellular polymers, the range of extracellular polymers is vast (Rehm, 2010). Four major classes of polymers produced by bacteria are

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for the formation of biofilms as they have adequate soil moisture and nutrients, some of which are delivered by the plants, which promotes biofilm formation (Rodríguez-Navarro et al., 2007). Biofilm formation depends upon the bacterial density and diversity that reside inside the polymeric matrix, i.e., EPSs formed by bacteria themselves.

Extracellular polysaccharide-producing bacteria initially attach to the plant root as the first step in the process of biofilm formation. This attachment of bacteria to plant roots, which is the first phase, is reversible and involves an unspecific binding. In this process, three components are involved: are lectin protein, rhicadhesin (Ca12-binding protein), and bacterial polysaccharides. Lectin proteins are present at the tip of legume root hairs that recognize specific carbohydrates present on the bacterial surface and bind to them (Isken & Bont, 1998). The second step of attachment is irreversible in nature, in which the synthesis of bacterial cellulose fibrils happens after 8–16 hours of bacterial inoculation and is intervened by the surface polysaccharides of bacteria. Among the diverse plant factors that mediate the process of bacterial attachment, the most significant is plant lectin, which functions as receptors for the bacterial EPS attachment (Rodríguez-Navarro et al., 2007).

The EPSs produced by *Planomicrobium chinense* and *Bacillus cereus* were shown to have profound effects on plant growth and drought tolerance, as the rhizospheric soil moisture content was improved following PGPR inoculation up to 77% over control (Khan & Bano, 2019). Plants inoculated with EPS-producing bacteria showed a higher accumulation of proline, sugars, and free amino acids under water deficit stress (Khan & Bano, 2019; Naseem et al., 2018). Seed bacterization of maize with EPS-producing bacterial strains improved soil moisture contents, plant biomass, root and shoot length, leaf area, leaf protein, and sugar contents under drought stress conditions (Naseem et al., 2014). Khan et al., (2019) reported similar results in wheat plants grown under rainfed conditions. A novel bacterial surface polysaccharide isolated from R. 1. bv. viciae RBL5523 (Laus et al., 2006), mainly composed of glucose and mannose, galactose, and rhamnose, showed high binding affinity to the lectins of *Pisum sativum* and *Vicia sativa*. Some surface polysaccharides produced by bacterial strain R. 1. bv. viciae RBL5523 (Laus et al., 2006) have been shown to contain lipopolysaccharides, EPSs, cyclic glucans, and capsular polysaccharides. More research on bacterial attachment and factors affecting biofilm formation can be helpful in extending the applications of EPS-producing bacteria in agriculture and beyond.

Survival Mechanism of Extracellular Polysaccharide-Producing Bacteria Under Drought Stress

Bacterial response to drought stress depends upon stress intensity, bacterial species and their growth stages, and the duration of stress exposure. Physiological changes accounting for microbial survival under abiotic stress conditions include the formation of cysts, flock formation, melanin production, synthesis of poly-β-hydroxybutyrate, synthesis of EPS, and protection by ectomycorrhizal spore caps. Polysaccharides, being hygroscopic, uphold a higher water content compared to bulk soil, which ensures bacterial survival in their microenvironment under the decreasing water potential scenario. Rhizobacteria are reported to show enhanced EPS production with an increase in drought stress conditions compared to normal conditions indicating a response to be triggered by drought stress (Roberson & Firestone, 1992). Under water stress conditions, amount and composition of EPSs are reported to change as capsular polysaccharides of *Azospirillum brasilense* sp245 contained high-molecular weight carbohydrates, lipopolysaccharide–protein, and polysaccharide-lipid complexes that showed protection against extreme drought. Extracellular polysaccharide-producing bacteria ensure their survival under drought stress not only by producing exopolysaccharides (Sandhya et al., 2009), which protect them from desiccation, but also by regulating the diffusion of organic carbon under drought stress (Latif et al., 2022). Studies have shown that, besides EPS, the greater release of soluble carbohydrates by PGPR into the plant rhizospheric soil improves the survival efficiency of microorganisms under water-deficit conditions. Soil bacteria adopt different strategies to overcome soil desiccation, like they modify the structure of their membrane or synthesize EPS in order to ensure their existence during the conditions of low external water potential.

In a study done by Ilyas et al. (2020), 24 bacterial strains were tested, out of which *Bacillus subtilis* and *A. brasilense* producing good amounts of EPSs and osmolytes improved drought tolerance in wheat by retaining 97% water in the matrix, which protected the bacteria as well as plants from desiccation. Colonization of EPS-producing bacteria like *Azospirillum* and *Pseudomonas* has shown a growth promotion effect on wheat and maize seedlings and other plants under low soil water content (Alvarez et al., 2008; Sandhya et al., 2009). *Pseudomonas putida* strain GAP-P45, an EPS-producing bacteria, is reported to form biofilm on sunflower root surfaces and confer drought tolerance. *P. putida* strain GAP-P45 showed extensive soil aggregation, and such plants whose root adhered soil had high relative water content in leaves (Sandhya et al., 2009). Few studies done on cowpea plants inoculated with *Bradyrhizobium* strain under drought conditions have correlated the amounts of EPS produced to the level of tolerance observed under drought conditions (Skvortsov & Ignatov, 1998).

Many microbes and plants survive up to 99% water loss during long durations of desiccation (Welsh, 2000), as these microbes form nodules under desert conditions. Literature is well documented with free-living rhizobia (saprophytes) capable of surviving under low water potential (Vardharajula et al., 2011). Most of the drought-resistant plants have shown deeper root penetration, heavier roots, and numerous primary and secondary roots, which indicate a greater rhizosphere volume that can hold a higher microbial population enduring drought tolerance. The ratio of root/shoot increases under drought conditions as roots are less vulnerable to water deficiency than shoots (Wu & Xia, 2006). Extracellular polysaccharides-producing microbes can be exploited to increase the drought tolerance capacity of plants by increasing their population density in the rhizospheric zone of plants.

Drought stress is generally accompanied by salinity and nutrient imbalance, thereby adversely affecting plant growth and crop production in cultivated areas worldwide. Plant productivity under such conditions is considerably reduced due to osmotic stress, membrane destabilization, and the partial closure of stomata. Soil salinity and drought together considerably reduce plant growth, photosynthetic capacity, protein synthesis, energy and lipid metabolism, and the total nitrogen contents (Upadhyay et al., 2011).

Extracellular polysaccharides-producing plant growth-promoting rhizobacteria can significantly enhance the volume of soil macropores and rhizosphere soil aggregation, resulting in increased water and fertilizer availability to inoculated plants. Extracellular polysaccharides producing PGPR also bind cations, including Na^+. Therefore, an increase in the population density of EPS-producing bacteria in the root zone is advantageous as it reduces the content of available Na^+ for plant uptake and in so doing alleviates salt stress in plants growing in saline environments (Upadhyay, 2011).

Mechanisms of Microbial Extracellular Polysaccharides on Soil Restructuring and Drought Tolerance
The tripartite interactions among the soil, plant roots, and bacteria in the rhizosphere lead to changes in soil physicochemical and structural properties (Berg & Smalla, 2009). Extracellular polysaccharide-producing microorganisms residing in soil contribute immensely in maintaining soil health and quality, as these polysaccharides attach to the particles of soil, forming macroaggregates of diameter >250 μm and micro aggregates of <250 μm (Oades, 1993). Bacterial EPSs have been studied extensively in the rhizosphere for their function in moisture retention. Slime materials and capsular EPSs released by microbes in soil may be adsorbed through the clay surfaces via cation bridges, the van der Waal's force, hydrogen bonding, and the anion absorption process, thereby providing a protective barrier surrounding soil aggregates. Furthermore alginate, a tiny polysaccharide existing as a biofilm, helps to maintain a hydrated microenvironment by water retention and drying at a slower pace than the surrounding environment, thus protecting plant roots and microorganisms from desiccation (Fadiji et al., 2022). Crops primed with bacteria capable of producing EPSs show enhanced resilience to moisture stress (Ojuederie et al., 2019). Treatment of the bacteria strain *B. subtilis* strain UD1022 increased soil water retention and reduced unsaturated hydraulic conductivity and evaporation, as measured through the HYPROP measurements and neutron radiography imaging. Scanning electron microscope and light microscope imaging of the control sand particles showed clean surfaces, whereas rod-shaped bacteria cells were found distributed in a continuous and thick layer of dried biofilm covering UD1022-treated sand particles. Bridier et al., (2013) observed in SEM images that bacterial cells of *B. subtilis* were embedded in mucoid-like structures in a hydrated matrix, and upon gradual dehydration, the cells were connected by a dense and oriented network of fibers. The mucus material and the fibrous skeleton under dehydrated conditions were identified as EPS (Branda et al., 2006; Kumar et al., 2012). Volk et al. (2016) also reported a reduction in both saturated and unsaturated hydraulic conductivity in soil samples after incubation with *Pseudomonas*. Mathematical models have been developed to take into account the effects of EPS or mucilage on soil water retention and hydraulic conductivity. In a composite model treating soil phase and EPS as separate media, the water content or hydraulic conductivity at any given potential was found as a linear superposition of that in each phase (Rockhold et al., 2002). Rosenzweig et al., (2012) found that the dominant mechanism for increased water retention was EPS' distinct water holding capacity. Kroener et al. (2018) observed that mucilage occupies small pores and creates additional potential during drying, so that water retention increases, especially under dry conditions. Carles Brangarí et al. (2017), in a more complex model, found that the swelling properties of EPSs lead to soil pore size change. All these modeling results indicate that small amounts of EPS or mucilage could lead to significant changes in water retention and hydraulic properties. The cross-linked and compact EPS matrix behaves like a sponge and is capable of absorbing water at an amount of tens (xanthan or pure bacterial EPS) or hundreds (root mucilage of maize) of times its dry weight (Zheng et al., 2018). Pure xanthan can hold 50–70 g of water per gram of xanthan while maintaining structural coherence (Chenu & Roberson, 1996). Flemming and Wingender (2010) reported that EPSs are hygroscopic and can retain water entropically rather than through specific water-binding mechanisms. Soils with different textures responded to bacterial EPSs or mucilage treatment differently, indicating that other mechanisms might have also played a role in increasing soil water retention (Benard et al., 2019). Filament networks formed by EPSs in between soil particles not only creates additional surface area but also increases the surface roughness, and it is important to note that surface roughness increases water film thickness. As EPSs are generally composed of polymeric substances, they exhibit a larger viscosity compared to water, thus increasing flow resistance. The viscous biofilm produced by Strain 3610 *B. subtilis* cells measured at an air–liquid interface was 200 times higher than pure water (Angelini et al., 2009). Overall, it has been estimated that the effect of EPSs on water retention and hydraulic conductivity is twofold, as the retained water is less mobile due to higher viscosity, and as a result, there are more saturated soil pores at the same potential due to reduced surface tension (Zheng et al., 2018). Network bridging of the soil pore space through EPSs is a universal strategy for plants and bacteria to engineer their own soil micro-hydrological niches where stable conditions for life can be preserved under drought (Benard et al., 2019).

Biofilm formation involving the transportation of EPS components from the microbial cell to the surface is regulated by quorum sensing. Quorum sensing process regulates cell–cell communication through specific gene expression in a cell density-dependent manner (Dutta et al., 2022). The process may, however, differ in the diverse bacterial forms. Maintenance of adequate soil structure and porosity is important as it aids in root growth, helping the plant explore a greater soil volume for nutrients and water. The EPSs produced by the rhizobacteria help in the formation of biofilm or sheath around the roots, which not only helps in holding the soil but also provides an active site for microbial interactions leading to nutrient recycling and its availability along with the flow of water to the plants (Kohler et al., 2008). Soil water potential acts as a key parameter in determining the availability of water, oxygen, and soil nutrients to the plants as well as microorganisms residing in the soil. Relative water content (RWC) in leaves is a measure of plant water status. Decreased RWC causes closure of stomata, leading to decreased CO_2 assimilation in plants, resulting in poor growth. While ample literature is focused on plants' physiological and yield parameters affected by EPS, studies lag on quantifying the effects of microbial EPSs on the RWC of leaves.

Mycorrhizal Interactions with Plants and Its Significance
Arbuscular mycorrhizal fungi forming symbiotic association with the root systems of 80% of terrestrial plants belong to the phylum Glomeromycota. Several mechanisms are involved in this symbiotic association that helps plant to survive even under stressful conditions, like enhanced growth through nutrient uptake, prevention of oxidative damage, reduced ion toxicity, and improving photosynthesis through osmotic adjustments. Arbuscular
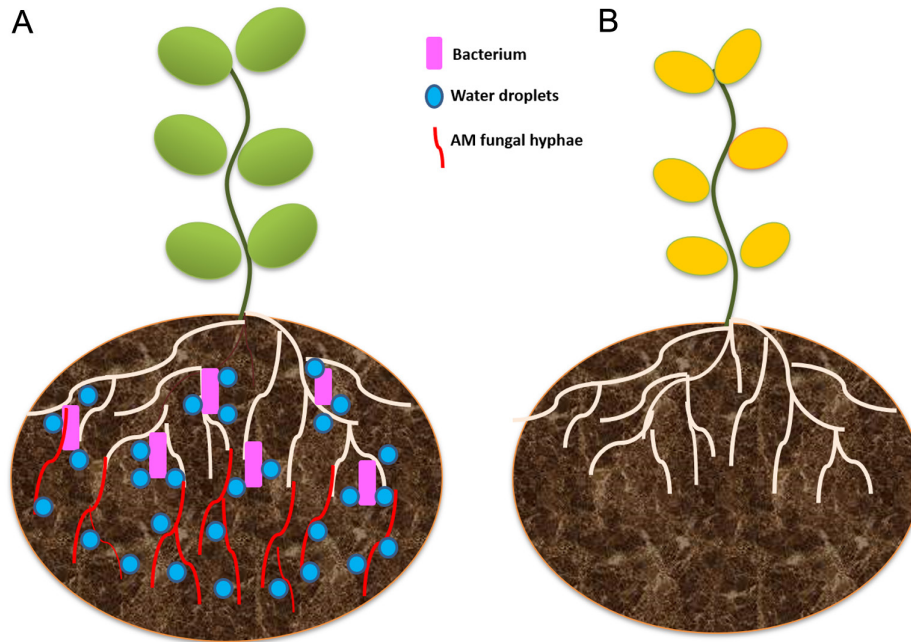
Figure 2.
Water Status in Rhizospheric Soil. (A) In the Presence of Microbes. (B) In the Absence of Microbes.

mycorrhizal fungi are key determinants of soil quality and are well recognized in processes of nutrient cycling and soil aggregation (Miller & Jastrow, 2000). The commonly occurring genera of AMF are *Glomus, Gigaspora, Scutellospora, Acaulospora,* and *Entrophospora*. Arbuscular mycorrhizal fungi inside the root form the intraradical mycelium, consisting of hyphae and other fungal structures, such as arbuscules, which are the sites of nutrient and carbon exchange between the symbionts, and vesicles, which help in fungal lipid storage. This intraradical mycelium is well extended outside the root, as is the extraradical mycelium in the soil, where it forms spores. The intraradical mycelium of soil mycorrhizal fungi inserted into the root cortex of the host plants assists in improving water relations, photosynthesis rates, and drought responses. It is the extraradical mycelium that plays a central role in contributing to soil quality. Arbuscular mycorrhiza formation results in an ecological niche for roots to be more accessible to water resources, as the fungal hyphae can penetrate soil pores inaccessible to the root hairs. They result in altering the root architecture, resulting in increased water uptake even at low soil moisture levels. The extraradical fungal hyphae is also capable of exploring water and nutrients beyond the depletion zone, as depicted in Figure 2.

Arbuscular mycorrhiza symbiosis not only enhances the acquisition of major plant nutrients like phosphate, nitrogen, and sulfur but even trace elements like zinc and copper. Arbuscular mycorrhiza colonization is also corelated with an increase in the activities of certain enzymes that help in the hydrolysis and mobilization of nutrients. In alkaline soils, phosphorus (P) often forms complexes with Ca and Mg, rendering P unavailable for uptake by plants. Higher acid phosphatase in the mycorrhizosphere as compared to the rhizosphere of non-arbuscular mycorrhiza plants enables the hydrolysis and mobilization of P, which is easily taken up by the plants. Higher soil acid phosphatase activities in the mycorrhizosphere were also observed to be positively correlated to soil water content. Thus, an increase in soil acid phosphatase activity due to mycorrhiza partially alleviates plant drought stress in plants (Wu et al., 2006). Arbuscular mycorrhiza symbiosis increases the units of photosynthesis, increasing the rates of photosynthetic storage and export in the plants. After infection in host plants, arbuscular mycorrhiza symbiosis incites a more powerful ROS scavenging system, which reduces the destruction of biomolecules at the cellular level under water stress conditions. Arbuscular mycorrhiza symbiotic plants exposed to water stress have been reported to show lower lipid peroxidation than nonmycorrhizal plants. Arbuscular mycorrhizal fungi protect host plants against oxidative damage through increase in enzymatic and nonenzymatic antioxidants. Increased enzymatic antioxidants, i.e., peroxidase and catalase, and alleviating ROS breakage are some of the methods of protecting arbuscular mycorrhiza plant organisms from oxidative bursts under water stress (Li et al., 2019).

Mycorrhizal Glomalin in Shaping Soil Structure
The soil structure reflects the soil biota to a large extent. Soil structure and biota are important aspects of the biogeochemical cycling process, even offering resistance to soil erosion. Soil aggregation is a complex process in which numerous microorganisms secreting various binding agents play a vital role (Miller & Jastrow, 2000). Arbuscular mycorrhizal fungi are ubiquitous soil organisms, and their relatively persistent hyphae and their products make AMF important contributors as longer-term aggregate stabilizers (Miller & Jastrow, 2000). Among all soil factors, AMF hyphae have a direct effect on soil aggregation through the production of glomalin protein, which helps in soil binding. The role of AMF in soil engineering has mostly been studied with respect to soil aggregation, as these aggregates physically protect the carbon inside and contribute to the soil carbon pool. Soil organic matter, which is related to carbon content, has a multifarious influence on soil quality, including water-holding capacity and nutrient storage capacity. The various roles of AMF in plant well-being, soil engineering, and ecosystem establishment is depicted in Figure 3.
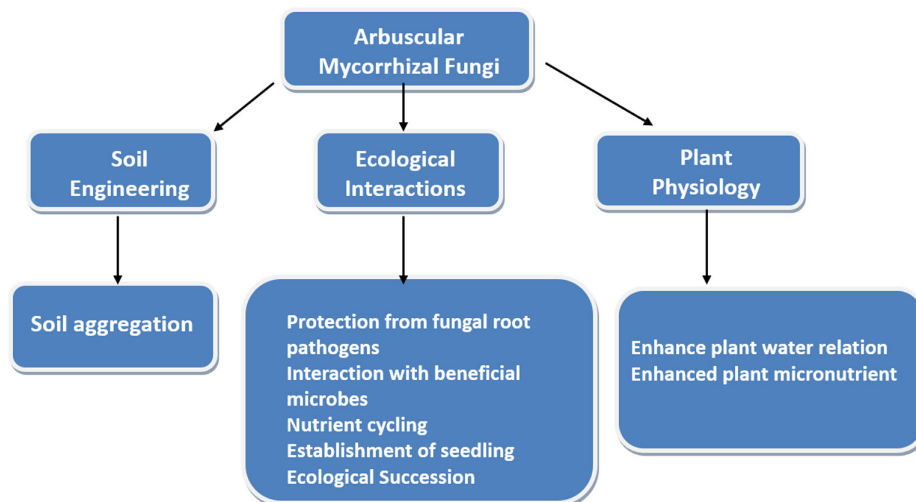
Figure 3.
Role of Arbuscular Mycorrhizal Fungi in Soil Engineering and Ecosystem Establishment.

Concentration of glomalin-related soil protein (GRSP) in soil has been positively correlated with aggregate water stability (Rillig, 2004). As GRSP has a slow turnover rate, it immensely contributes to soil aggregation in the long term. However, few studies done through conventional disintegrating forces show that GRSP concentration is positively correlated with soil aggregate water stability only to an extent and beyond a certain saturation level; additional deposition of GRSP does not remarkably increase the soil aggregate water stability (Kemper & Rosenau, 1986). Further, when talking of large-scale managed agroecosystems where water stability is quite low, the addition of low levels of GRSP shows a linear relationship to water stability (Wright & Upadhyaya, 1998). A path analysis experiment done in California grassland showed AMF hyphae and its products, i.e., glomalin, as significant contributors to soil aggregate water stability (Rillig, 2004). Of the soil protein pool, GRSP shows a slow turnover time, which makes it an important compound in soil aggregation. Few data suggest that glomalin is retained in the hyphal or spore wall instead of being secreted in the soil (Driver et al., 2005). It is only after the hyphal turnover that it gets deposited into the soil. Glomalin-related soil protein remained after >400 days in soil under lab incubation conditions in an experiment conducted on Ohio, USA, soils. A study conducted in western Montana grassland on seasonal variation in GRSP concentrations exhibited minor temporal coefficient variations, but some GRSP fractions showed statistically significant changes (Lutgen et al., 2003). Revealing the molecular biology of glomalin can be of great help in tracing the trajectory of this important soil-binding protein. Many studies have reported AMF as a determining factor in plant species diversity (van der Heijden et al., 1998) at the ecosystem level. In agroecosystems AMF diversity and performance are greatly influenced by tillage, application of biocides, cropping sequences (nonmycorrhizal hosts), fertilization, and genotype. It has been clearly demonstrated that the soil GRSP pools are negatively affected by agricultural practices like crop rotation and tillage (Wang et al., 2011). Glomalin-related soil protein pools are also sensitive to environmental factors like elevated atmospheric CO_2 concentration which increases the level of GRSP, or warming, which brings down the GRSP concentration in the soil (Rillig, 2004). A recent critical review on the occurrence and functioning of AMF in agroecosystems (Ryan & Graham, 2002) has concluded the negative influence of modern agroecosystem management practices on diversity and functional aspects of AMF. More research done on the role of GRSP in soil aggregation beyond the 1- to 2-mm size class can help in better understanding.

Managing GRSP concentration in soil can be a promising approach to improve soil structure and quality, not only in agricultural soil but also in degraded ecosystems. Preliminary research indicates that glomalin amounts in soils can be manipulated by changing the composition of the arbuscular mycorrhiza community or altering the arbuscular mycorrhiza physiology, which is well correlated with the physiological status of the host species (Rillig, 2004). Arbuscular mycorrhizal fungi clearly differs in many of their life history traits, and it has been observed that different AMF species produce varying amounts of GRSP, a character that can be explored to increase the utility of marginal lands and bring them under agricultural purpose by inhabiting AMF species with a high GRSP production rate.

Conclusion

Plants can be made more tolerant to drought stress by increasing EPSs and producing microbial population density in the root zone. Extracellular polysaccharide-producing PGPR and AMF are important biotic factors that influence soil quality and plant growth through their direct effects on soil structure and indirectly through their effects on host physiology and ecological interactions. Glomalin, a hyphal product, contributes to soil aggregation and water stability across different types of soils, and thus the AMF community is an important regulator helpful in soil engineering. Managing an appropriate microbial consortium in soil can be promising in overcoming the adverse effects of deficit irrigation in cropping.

References

Abdalla, A. K., Ayyash, M. M., Olaimat, A. N., Osaili, T. M., Al-Nabulsi, A. A., Shah, N. P., & Holley, R. (2021). Exopolysaccharides as antimicrobial agents: Mechanism and spectrum of activity. *Frontiers in Microbiology*, *12*, 664395. [CrossRef]

Alvarez, S., Marsh, E. L., Schroeder, S. G., & Schachtman, D. P. (2008). Metabolomic and proteomic changes in the xylem sap of maize under drought. *Plant, Cell and Environment*, *31*(3), 325–340. [CrossRef]

Angelini, T. E., Roper, M., Kolter, R., Weitz, D. A., & Brenner, M. P. (2009). *Bacillus subtilis* spreads by surfing on waves of surfactant. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(43), 18109–18113. [CrossRef]

Bai, B., Liu, W. D., Qiu, X. Y., Zhang, J., Zhang, J. Y., & Bai, Y. (2022). The root microbiome: Community assembly and its contributions to plant fitness. *Journal of Integrative Plant Biology*, *64*(2), 230–243. [CrossRef]

Benard, P., Zarebanadkouki, M., Brax, R., Kaltenbach, I., Jerjen, F., Marone, E., Couradeau, V. J. M. N. L., Felde, K., A., & Carminati, A. (2019). Micro-hydrological niches in soils: How mucilage and EPS alter the biophysical properties of the rhizosphere and other biological hotspots. *Vadose Zone Journal*, *18*, 180211. [CrossRef]

Berg, G., & Smalla, K. (2009). Plant species and soil type cooperatively shape the structure and function of microbial communities in the rhizosphere. *FEMS Microbiology Ecology*, *68*(1), 1–13. [CrossRef]

Branda, S. S., Chu, F., Kearns, D. B., Losick, R., & Kolter, R. (2006). A major protein component of the *Bacillus subtilis* biofilm matrix. *Molecular Microbiology*, *59*(4), 1229–1238. [CrossRef]

Bridier, A., Meylheuc, T., & Briandet, R. (2013). Realistic representation of *Bacillus subtilis* biofilms architecture using combined microscopy (CLSM, ESEM and FESEM). *Micron*, *48*, 65–69. [CrossRef]

Carles Brangarí, A., Sanchez-Vila, X., Freixa, A., Romaní, A. M., Rubol, S., & Fernàndez-Garcia, D. (2017). A mechanistic model (BCC-PSSICO) to predict changes in the hydraulic properties for bio-amended variably saturated soils. *Water Resources Research*, *53*(1), 93–109. [CrossRef]

Chenu, C., & Roberson, E. B. (1996). Diffusion of glucose in microbial extracellular polysaccharide as affected by water potential. *Soil Biology and Biochemistry*, *28*(7), 877–884. [CrossRef]

Concórdio-Reis, P., Reis, M. A. M., & Freitas, F. (2020). Biosorption of heavy metals by the bacterial exopolysaccharide FucoPol. *Applied Sciences*, *10*(19), 6708. [CrossRef]

Driver, J. D., Holben, W. E., & Rillig, M. C. (2005). Characterization of glomalin as a hyphal wall component of arbuscular mycorrhizal fungi. *Soil Biology and Biochemistry*, *37*(1), 101–106. [CrossRef]

Dutta, A., Banerjee, S., Dinda, S., Chowdhury, I., Haldar, S., & Bandyopadhyay, S. (2022). A critical analysis on the roles of exopolysaccharides and ACC deaminase in salinity stress tolerance in crop plants. *Biocatalysis and Agricultural Biotechnology*, *42*. [CrossRef]

Ercole, C., Cacchio, P., Botta, A. L., Centi, V., & Lepidi, A. (2007). Bacterially induced mineralization of calcium carbonate: The role of exopolysaccharides and capsular polysaccharides. *Microscopy and Microanalysis*, *13*(1), 42–50. [CrossRef]

Fadiji, A. E., Santoyo, G., Yadav, A. N., & Babalola, O. O. (2022). Efforts towards overcoming drought stress in crops: Revisiting the mechanisms employed by plant growth-promoting bacteria. *Frontiers in Microbiology*, *13*, 962427. [CrossRef]

Flemming, H. C., & Wingender, J. (2010). The biofilm matrix. *Nature Reviews. Microbiology*, *8*(9), 623–633. [CrossRef]

Goswami, D., Thakker, J. N., & Dhandhukia, P. C. (2016). Portraying mechanics of plant growth promoting rhizobacteria (PGPR): A review. *Cogent Food and Agriculture*, *2*(1). [CrossRef]

Hakim, S., Naqqash, T., Nawaz, M. S., Laraib, I., Siddique, M. J., Zia, R., Mirza, M. S., & Imran, A. (2021). Rhizosphere engineering with plant growth-promoting microorganisms for agriculture and ecological sustainability. *Frontiers in Sustainable Food Systems*, *5*, 617157. [CrossRef]

Ilyas, N., Mumtaz, K., Akhtar, N., Yasmin, H., Sayyed, R. Z., Khan, W., El Enshasy, H. A. E., Dailin, D. J., Elsayed, E. A., & Ali, Z. (2020). Exopolysaccharides producing bacteria for the amelioration of drought stress in wheat. *Sustainability*, *12*(21), 8876. [CrossRef]

Isken, S., & de Bont, J. A. (1998). Bacteria tolerant to organic solvents. *Extremophiles: Life under Extreme Conditions*, *2*(3), 229–238. [CrossRef]

Kemper, W. D., & Rosenau, R. C. (1986). Aggregate stability and size distribution. In A. Klute (Ed.). *Methods of Soil Analysis* (pp. 425–442). Australian Society of Anaesthetists. [CrossRef]

Khan, N., & Bano, A. (2019). Exopolysaccharide producing rhizobacteria and their impact on growth and drought tolerance of wheat grown under rainfed conditions. *PLoS One*, *14*(9), e0222302. [CrossRef]

Khan, N., Bano, A., & Babar, M. A. (2017). The root growth of wheat plants, the water conservation and fertility status of sandy soils influenced by plant growth promoting rhizobacteria. *Symbiosis*, *72*(3), 195–205. [CrossRef]

Kimmel, S. A., & Roberts, R. F. (1998). Development of a growth medium suitable for exopolysaccharide production by *Lactobacillus delbrueckii* ssp. *bulgaricus* RR. *International Journal of Food Microbiology*, *40*(1–2), 87–92. [CrossRef]

Kohler, J., Hernández, J. A., Caravaca, F., & Roldán, A. (2008). Plant-growth promoting rhizobacteria and arbuscular mycorrhizal fungi modify alleviation biochemical mechanisms in water-stressed plants. *Functional Plant Biology*, *35*(2), 141–151. [CrossRef]

Kroener, E., Holz, M., Zarebanadkouki, M., Ahmed, M., & Carminati, A. (2018). Effects of mucilage on rhizosphere hydraulic functions depend on soil particle size. *Vadose Zone Journal*, *17*(1), 1–11. [CrossRef]

Latif, M., Bukhari, S. A. H., Alrajhi, A. A., Alotaibi, F. S., Ahmad, M., Shahzad, A. N., Dewidar, A. Z., & Mattar, M. A. (2022). Inducing drought tolerance in wheat through exopolysaccharide producing rhizobacteria. *Agronomy*, *12*(5), 1140. [CrossRef]

Laus, M. C., Logman, T. J., Lamers, G. E., van Brussel, A. A., Carlson, R. W., & Kijne, J. W. (2006). A novel polar surface polysaccharide from *Rhizobium leguminosarum* binds host plant lectin. *Molecular Microbiology*, *59*(6), 1704–1713. [CrossRef]

Li, J., Meng, B., Chai, H., Yang, X., Song, W., Li, S., Lu, A., Zhang, T., & Sun, W. (2019). Arbuscular Mycorrhizal fungi alleviate drought stress in C_3 (*Leymus chinensis*) and C_4 (*Hemarthria altissima*) grasses via altering antioxidant enzyme activities and photosynthesis. *Frontiers in Plant Science*, *10*, 499. [CrossRef]

Lutgen, E. R., Muir-Clairmont, D., Graham, J., & Rillig, M. C. (2003). Seasonality of arbuscular mycorrhizal hyphae and glomalin in a western Montana grassland. *Plant and Soil*, *257*(1), 71–83. [CrossRef]

Miller, R. M., & Jastrow, J. D. (2000). Mycorrhizal fungi influence soil structure. In Y. Kapulnik & D. D. Douds (Eds.). *Arbuscular mycorrhizae: Molecular biology and physiology* (pp. 3–18). Kluwer Academic Press.

Nadeem, S. M., Ahmad, M., Tufail, M. A., Asghar, H. N., Nazli, F., & Zahir, Z. A. (2021). Appraising the potential of EPS-producing rhizobacteria with ACC-deaminase activity to improve growth and physiology of maize under drought stress. *Physiologia Plantarum*, *172*(2), 463–476. [CrossRef]

Naseem, H., Ahsan, M., Shahid, M. A., & Khan, N. (2018). Exopolysaccharides producing rhizobacteria and their role in plant growth and drought tolerance. *Journal of Basic Microbiology*, *58*(12), 1009–1022. [CrossRef]

Naseem, H., & Bano, A. (2014). Role of plant growth-promoting rhizobacteria and their exopolysaccharide in drought tolerance of maize. *Journal of Plant Interactions*, *9*(1), 689–701. [CrossRef]

Nguyen, P. T., Nguyen, T. T., Bui, D. C., Hong, P. T., Hoang, Q. K., & Nguyen, H. T. (2020). Exopolysaccharide production by lactic acid bacteria: The manipulation of environmental stresses for industrial applications. *AIMS Microbiology*, *6*(4), 451–469. [CrossRef]

Nielsen, P. H., & Jahn, A. (1999). *Extraction of EPS. Microbial extracellular polymeric substances* (pp. 49–72). Springer.

Oades, J. M. (1993). *The role of biology in the formation, stabilization and degradation of soil structure. Soil Structure/soil biota interrelationships. International agricultural centre* (pp. 377–400). Elsevier.

Ojuederie, O. B., Olanrewaju, O. S., & Babalola, O. O. (2019). Plant growth promoting rhizobacterial mitigation of drought stress in crop plants: Implications for sustainable agriculture. *Agronomy*, *9*(11), 712. **[CrossRef]**

Prasad, J. K., & Raghuwanshi, R. (2022). Mechanisms of multifarious soil microbial enzymes in plant growth promotion and environmental sustainability. In M. Shah & P. Verma (Eds.). *Bioprospecting of Microbial Diversity: Challenges and outlook towards agricultural, industrial and environmental domains*. Elsevier.

Prasad, J. K., Dey, R., & Raghuwanshi, R. (2022). Exopolysaccharide-producing rhizospheric bacteria enhance yield via promoting wheat (*Triticum aestivum* L.) growth at early stages. *Microbiology*, *91*(6), 757–769. **[CrossRef]**

Rehm, B. H. (2010). Bacterial polymers: Biosynthesis, modifications and applications. *Nature Reviews. Microbiology*, *8*(8), 578–592. **[CrossRef]**

Rillig, M. C. (2004). Arbuscular mycorrhizae, glomalin and soil aggregation. *Canadian Journal of Soil Science*, *84*(4), 355–363. **[CrossRef]**

Roberson, E. B., & Firestone, M. K. (1992). Relationship between desiccation and exopolysaccharide production in a soil *Pseudomonas* sp. *Applied and Environmental Microbiology*, *58*(4), 1284–1291. **[CrossRef]**

Rockhold, M. L., Yarwood, R. R., Niemet, M. R., Bottomley, P. J., & Selker, J. S. (2002). Considerations for modeling bacterial-induced changes in hydraulic properties of variably saturated porous media. *Advances in Water Resources*, *25*(5), 477–495. **[CrossRef]**

Rodríguez-Navarro, D. N., Dardanelli, M. S., & Ruíz-Saínz, J. E. (2007). Attachment of bacteria to the roots of higher plants. *FEMS Microbiology Letters*, *272*(2), 127–136. **[CrossRef]**

Rosenzweig, R., Shavit, U., & Furman, A. (2012). Water retention curves of biofilm-affected soils using xanthan as an analogue. *Soil Science Society of America Journal*, *76*(1), 61–69. **[CrossRef]**

Ryan, M. H., & Graham, J. H. (2002). Is there a role for arbuscular mycorrhizal fungi agriculture? *Plant and Soil*, *244*(1/2), 263–271. **[CrossRef]**

Sandhya, V. Z., Grover, M., Grover, M., Reddy, G., & Venkateswarlu, B. (2009). Alleviation of drought stress effects in sunflower seedlings by the exopolysaccharides producing *Pseudomonas putida* strain GAP-P45. *Biology and Fertility of Soils*, *46*(1), 17–26. **[CrossRef]**

Schnurr, P. J., & Allen, D. G. (2015). Factors affecting algae biofilm growth and lipid production: A review. *Renewable and Sustainable Energy Reviews*, *52*, 418–429. **[CrossRef]**

Skvortsov, I. M., & Ignatov, V. V. (1998). Extracellular polysaccharides and polysaccharide-containing biopolymers from *Azospirillum* species: Properties and the possible role in interaction with plant roots. *FEMS Microbiology Letters*, *165*(2), 223–229. **[CrossRef]**

Sutherland, I. W. (1977). *Bacterial exopolysaccharide their nature and production. Surface carbohydrates of the prokaryotic cell* (pp. 27–96). Academic Press.

Upadhyay, S. K., Singh, J. S., & Singh, D. P. (2011). Exopolysaccharide producing plant growth-promoting rhizobacteria under salinity condition. *Pedosphere*, *21*(2), 214–222. **[CrossRef]**

van der Heijden, M. G. A., Klironomos, J. N., Ursic, M., Moutoglis, P., Streitwolf-Engel, R., Boller, T., Wiemken, A., & Sanders, I. R. (1998). Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. *Nature*, *396*(6706), 69–72. **[CrossRef]**

Vardharajula, S., Zulfikar Ali, S., Grover, M., Reddy, G., & Bandi, V. (2011). Drought tolerant plant growth promoting *Bacillus* spp.: Effect on growth, osmolytes, and antioxidant status of maize under drought stress. *Journal of Plant Interactions*, *6*(1), 1–14. **[CrossRef]**

Volk, E., Iden, S. C., Furman, A., Durner, W., & Rosenzweig, R. (2016). Biofilm effect on soil hydraulic properties: Experimental investigation using soil-grown real biofilm. *Water Resources Research*, *52*(8), 5813–5828. **[CrossRef]**

Wang, P., Liu, J. H., Xia, R. X., Wu, Q. S., Wang, M. Y., & Dong, T. (2011). Arbuscular mycorrhizal development, glomalin-related soil protein (GRSP) content, and rhizospheric phosphatase activity in citrus orchards under different types of soil management. *Journal of Plant Nutrition and Soil Science*, *174*(1), 65–72. **[CrossRef]**

Welsh, D. T. (2000). Ecological significance of compatible solute accumulation by microorganisms: From single cells to global climate. *FEMS Microbiology Reviews*, *24*(3), 263–290. **[CrossRef]**

Wright, S. F., & Upadhyaya, A. (1998). A survey of soils for aggregate stability and glomalin, a glycoprotein produced by hyphae of arbuscular mycorrhizal fungi. *Plant and Soil*, 97–107.

Wu, Q. S., & Xia, R. X. (2006). Arbuscular mycorrhizal fungi influence growth, osmotic adjustment and photosynthesis of citrus under well watered and water stress conditions. *Journal of Plant Physiology*, *163*(4), 417–425. **[CrossRef]**

Zheng, W., Zeng, S., Bais, H., LaManna, J. M., Hussey, D. S., Jacobson, D. L., & Jin, Y. (2018). Plant growth-promoting rhizobacteria (PGPR) reduce evaporation and increase soil water retention. *Water Resources Research*, *54*(5), 3673–3687. **[CrossRef]**