

Use of Rhizosphere Microorganisms in Plant Production – A Review Study

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ABSTRACT

Minimizing or neutralizing the effects of environmental stresses on crop plants, protecting against pests and diseases, and at the same time ensuring optimal plant growth and development are currently the most important tasks faced by growers and plant producers around the world. Nowadays, the goal is to limit the use of chemicals as much as possible to protect the environment and improve the quality of food. The interest in the use of beneficial rhizosphere microorganisms is becoming global, as it can represent an environmentally friendly alternative to chemicalization in the era of threats to crop cultivation in the modern world (climate change, drought, salinity, introduction of plant pests).

Keywords: PGPM, PGPR, PGPF, AMF, environmental stresses

INTRODUCTION

The microbiome communities living in an environment affects the health of plants, people, and other living things. In plants, different microbiomes colonize in various niches, in phyllosphere, endosphere (in the tissues) and rhizosphere (Berendsen et al. 2012).

The rhizosphere is the root zone where the interactions occurring at the plant–microorganism–soil level are influenced by a number of chemical (pH, nutrient content, exudates), physical (temperature, water availability, soil structure), and biological (bacteria and fungi) factors (Mimmo et al. 2018).

Rhizosphere microbial communities and their interactions have been the subject of research for many years, aimed at determining their influence on plant development (Philippot et al. 2013, Berg et al. 2014). Many authors showed that microorganisms bring many benefits to cultivated plants, such as: nutrient uptake (Berendsen et al. 2012), protection against soil pathogens (Mendes et al. 2013), and resistance to environmental stresses (Pérez-Jaramillo et al. 2015). The rhizosphere is a

site of microbiological activity contributed to by bacteria, fungi, protozoa, nematodes, algae, and archaea (Lakshmanan et al. 2014). Plant Growth Promoting Microorganisms (PGPM) – bacteria and fungi, including mycorrhizal fungi, are the most widely studied groups of microorganisms.

Plant Growth Promoting Microorganisms can be divided into Plant Growth Promoting Rhizobacteria – PGPR and Plant Growth Promoting Fungi – PGPF (Mishra et al. 2017).

PGPR are microorganisms essentially present in the rhizosphere and include the following strains of bacteria: *Acinetobacter*, *Alcaligenes*, *Allorhizobium*, *Arthrobacter*, *Azorhizobium*, *Azospirillum*, *Bacillus*, *Bradyrhizobium*, *Burkholderia*, *Enterobacter*, *Erwinia*, *Flavobacterium*, *Frankia*, *Mezorhizobium*, *Pseudomonas*, *Rhizobium* and *Sinorhizobium* (Sharma et al. 2016, Patel et al. 2016, Bashan et al. 2016, Lal et al. 2016). According to Chauhan et al. (2015), the group of Plant Growth Promoting Bacteria also includes the recently used strains, such as: *Pantoea*, *Methylobacterium*, *Exiguobacterium*, *Paenibacillus* and *Azoarcus*. PGPR contribute to plant growth through direct or indirect mechanisms. Any

mechanism that protects a plant against infections (biotic stress) or helps it develop under abiotic stress is an indirect mechanism. In contrast, the direct mechanism affects the plant growth through the supply of nutrients or the production of plant growth regulators (Goswami et al. 2016).

The interaction with PGPF also proves to be extremely beneficial for the flora. Fungi of the genera such as *Aspergillus*, *Fusarium*, *Penicillium*, *Piriformospora*, *Phoma* and *Trichoderma* are the strains most used in research (Hossain et al. 2017, Javaid et al. 2019). Comparison of the results of various experiments shows that the interactions at the plant–PGPF level can have a positive effect on the aerial and underground plant organs. According to Akhtar and Javaid (2018), PGPF provide plants with protection against diseases by limiting the penetration by pathogens. Yadav et al. (2017) showed in their study that application of fungi to the soil increased nutrient availability to plants, thus increasing plant growth and crop yields.

Mycorrhizal symbiosis is the most common and widespread synergy between microorganisms and plants. As reported by Bonfante and Genre (2010), endophytic fungi (endomycorrhiza, arbuscular mycorrhiza – AM, Arbuscular Mycorrhizal Fungi – AMF) are a group of fungi of the *Glomeromycota* genera that form symbiotic relationships with over 90% of higher plant families. According to many authors, inoculation with AMF provides plants with tolerance to various environmental stresses such as salinity, water deficit, heavy metals in soil, and low or high temperatures.

The role of rhizosphere microorganisms in alleviating environmental stresses

Stress factors affect the growth and development of plants in agricultural and horticultural production. Light, water, and minerals are the factors regulating their growth, development and reproduction (Lata et al. 2018). However, when the access to them is disturbed, plants undergo physiological and morphological modifications to adapt to sudden changes (Shukla et al. 2012).

Abiotic stresses that affect the plant production efficiency include drought, salinity, hot and cold stress, as well as light stress. When listing the factors negatively affecting yielding, one cannot ignore the lack of nutrient availability in the soil, content of heavy metals, and the presence of plant pathogens (Lata and Gond 2019).

Plant growth under stress conditions can be enhanced by the use of stress-resistant rhizosphere microorganisms such as PGPR, PGPF and AMF (Nadeem et al. 2014). According to Spence and Bais (2015), these microorganisms enhance the plant development through, for example, regulation of the hormonal and nutritional balance, production of plant growth regulators, and induction of resistance to pathogens.

The role of rhizosphere microorganisms in alleviating the drought stress

The drought-induced stress is one of the most serious world problems, which reduces the crop production. Almost 30% of the Earth's soils are exposed to this stress (Calvo-Polanco et al. 2016). This stress has multidimensional influence on plants, from the phenological and morphological levels down to the molecular level (Anjum et al. 2011).

According to Lata and Prasad (2011) and Naveed et al. (2014), the water deficit causes many negative changes in plants such as decrease of chlorophyll concentration, disorders of photosynthetic apparatus, inhibition of photosynthesis and transpiration, increase in ethylene production and decrease in relative water content. The limited water content causes a decrease in the size of cells in tissues, disrupts membrane integrity, inhibits production of ROS in plants, and promotes leaf senescence (Tiwari et al. 2015, Kaur and Asthir 2016).

The rhizosphere microorganisms stimulate the growth of plants during drought stress by inducing various mechanisms such as production of plant growth regulators (IAA, cytokinins and ABA), production of bacterial exopolysaccharides (EPS), and synthesis of ACC deaminase (Farooq et al. 2009, Porcel et al. 2014).

Plant Growth Promoting Rhizobacteria have the ability to produce phytohormones that stimulate cell division and plant growth under the water deficit conditions (Kumar and Verma 2018). According to Goswami et al. (2015), IAA regulates differentiation of vascular tissues, stimulates cell division, and root and shoot growth under stress. Abscisic acid (ABA) alleviates the stress caused by water deficit through transcription and regulation of xylem transport to the aerial parts of plants (Jiang et al. 2013). Vardharajula et al. (2011) claim that the bacteria *Bacillus* sp., counted among the PGPR, reduce antioxidant activity,

but increase the synthesis of proline, free amino acids and production of sugars in plants.

According to Mena-Violante et al. 2006, Ruiz-Lozano et al., 2015, Yooyongwech et al. 2016 and Moradtalab et al. 2019, the mycorrhizal fungi alleviate drought stress in the cultivation of various species such as: pepper, lettuce, tomato, strawberry and sweet potato. It has been shown that symbiotic relationships with AMF can contribute to root growth, increase leaf surface area and plants biomass under water deficit (Gholamhoseini et al. 2013).

Inoculation with AMF affects the physiological characteristics of plants, e.g. stomatal conductance, leaf water potential (LWP), relative water content (RWC), and CO₂ assimilation (He et al. 2017, Chandrasekaran et al. 2019). According to Ludwig-Müller (2010), MF and PGPR, induce the synthesis of abscisic acid (ABA), which under stress conditions regulates some of physiological processes, e.g. stomatal conductance. Supplementary information is shown in the Table 1.

The role of rhizosphere microorganisms in alleviating salinity stress

Excessive soil salinity is a complex phenomenon, harmful to plants because it causes disorders of the ionic and osmotic homeostasis. It leads to a reduction in growth and development, and premature senescence of plants (Bojorquez-Quintal et al. 2014, Enebe and Babalola 2018, Julkowska and Testerink 2015). Salinity is mainly caused by Na⁺, Ca²⁺, K⁺ and also Cl⁻ and NO₃⁻ (Shrivastava and Kumar 2015). It reduces the microbiological activity of the soil, which is caused by ion toxicity and osmotic stress, which affect the reduction in growth of plant.

There have been many studies confirming that the inoculation with rhizosphere microorganisms alleviates the negative effects of salinity on various plants. PGPM can stimulate the growth of the plants that are exposed to salinity, by direct and indirect mechanisms. Rhizosphere bacteria reduce the effects of excessive soil salinity, also by producing the so-called biofilm (biological membrane) on the roots (Kasim et al. 2016).

Both PGPR and AMF help plants adapt to salinity, increasing the availability of nutrients, improving water uptake, increasing the efficiency of CO₂ assimilation, and the synthesis of osmoregulators and phytohormones (auxins, cytokinins, ethylene, gibberellins) (Hajiboland et al. 2010, Porcel et al. 2015, Hayat et al. 2010).

As reported by Choudhary et al. (2015), the PGPR that are studied in terms of their interaction with plant growth in salinity stress include *Ace-tobacter*, *Azospirillum*, *Bacillus*, *Pseudomonas*, *Rhizobium* and *Serratia*. Damodaran et al. (2013) demonstrated that *Bacillus pumilus* and *Bacillus subtilis* found in saline soil had tolerance to salt stress, through various mechanisms, e.g. synthesis of IAA, ACC deaminase, ammonia and hydrogen cyanide (HCN), and by phosphate solubilization or siderophore production. Bacilio et al. (2016), showed that inoculation with bacteria *Pseudomonas stutzeri* reduces the negative impact of excessive soil salinity on pepper plants.

Some authors reported the effectiveness of AMF in increasing the growth and yielding of plants in salinity (Talaat and Shawky 2014, Latef and Chaoxing 2014). For some plants, co-inoculation with mycorrhizal fungi (AMF) and saline-tolerant bacteria can also improve their salinity resistance. According to Krishnamoorthy et al. (2016), co-inoculation with *Rhizophagus intraradices* and *Massilia* sp. RK4 (bacteria) together with AMF (fungi) showed a significant effect on the tolerance to excessive soil salinity in maize plants. Supplementary information is shown in Table 2.

The role of rhizosphere microorganisms in alleviating temperature stress (heat stress, cold stress)

The constantly changing climate contributes to increasing the risk of temperature stress, a significant threat to the crop productivity worldwide (Kumar and Verma 2018). According to Wahid et al. (2007), Hasanuzzaman et al. (2013) and Zandalinas et al. (2018), heat stress significantly affects the biochemical and physiological traits of plants, development, growth and yielding (causing loss of vigour and inhibition of seed germination, smaller plant mass, wilting and leaf senescence, fruit damage and discoloration, as well as cell apoptosis and increased oxidative stress). At heat stress, plants accumulate antioxidants (ascorbate peroxidase, catalase), osmoprotectants, and Heat Shock Proteins (HSP) – HSP20, HSP 60, HSP70, HSP 90, HSP100 (Bokszczanin 2013, Qu et al. 2013, Kotak et al. 2007).

Zhuang et al. (2019), reported that the stress associated with low temperature affects a lot of biological processes, such as a damage to cell membranes and changes in the photosynthetic

Table 1. Responses of plants in water deficit to inoculation of different rhizosphere microorganisms

Microorganism	Plant species	Effect	Research author
Plant Growth Promoting Rhizobacteria (PGPR)			
<i>Pseudomonas libanensis</i> TR1 <i>Pseudomonas reactans</i> Ph3R3	<i>Brassica oxyrrhina</i> Coss.	plant growth, increase in leaf water content (LWC), increase in chlorophyll content	Ma et al. 2016a
<i>Proteus penneri</i> Pp1 <i>Pseudomonas aeruginosa</i> (Pa2) <i>Alcaligenes faecalis</i> (AF3)	maize (<i>Zea mays</i> L.)	increase in relative water content (RWC), increase in protein and sugar content, increase in proline content	Naseem and Bano 2014
<i>Trichoderma longibrachiatum</i>	wheat (<i>Triticum aestivum</i> L.)	increase in relative water content (RWC), increase in chlorophyll and proline content	Zhang et. al. 2016
<i>Azospirillum brasilense</i> Sp 245	thale cress (<i>Arabidopsis thaliana</i> (L.) Heynh.)	increase in plant yielding, increase in relative water content (RWC), increase in proline content	Cohen et. al. 2015
<i>Pseudomonas entomophila</i> BV-P13 <i>Pseudomonas stutzeri</i> GRFHAP-P14 <i>Pseudomonas putida</i> GAP-P45 <i>Pseudomonas syringae</i> GRFHYP5 <i>Pseudomonas monteilli</i> WAPP53	maize (<i>Zea mays</i> L.)	increase in proline, sugars and free amino acids content	Vardharajula et al. 2010
<i>Bacillus cereus</i> AR156 <i>Bacillus subtilis</i> SM21 <i>Serratia sp.</i> XY21	cucumber (<i>Cucumis sativus</i> L.)	activation of Induced Systemic Resistance (ISR), maintain photosynthetic performance, vigour and antioxidant activity	Wang et al. 2012
<i>Pseudomonas aeruginosa</i> GGRJ21	mung bean (<i>Vigna radiata</i> L.)	production of reactive oxygen species (ROS), increase in relative water content (RWC), increase in shoots, roots and dry matter	Sarma and Saikia 2014
Plant Growth Promoting Fungi (PGPF)			
<i>Trichoderma atroviride</i> ID20G	maize (<i>Zea mays</i> L.)	increase in fresh and dry root mass, increase in chlorophyll and carotenoid content, inhibition of lipid peroxidation, induction of antioxidant enzymes, decrease in hydrogen superoxide (H ₂ O ₂) content	Guler et al. 2016
<i>Exophiala sp.</i> LHL08	cucumber (<i>Cucumis sativus</i> L.)	abscisic acid (ABA), salicylic acid (SA) and gibberellin (GA) induction	Khan et al. 2011a
Arbuscular Mycorrhizal Fungi (AMF)			
<i>Rhizophagus irregularis</i> <i>Glomus intraradices</i>	lettuce (<i>Lactuca sativa</i> L.), tomato (<i>Lycopersicon esculentum</i> Mill.)	plant growth, indole-3-acetic acid production, increase in Photosystem II (PSII) performance	Ruiz-Lozano et al. 2015
<i>Acaulospora sp.</i> <i>Glomus sp.</i>	sweet potato (<i>Ipomoea batatas</i> (L.) Poir)	increase in efficiency of Photosystem II (PSII), increase in chlorophyll, proline and sugars content	Yooyongwech et al. 2016
<i>Rhizophagus clarus</i>	strawberry (<i>Fragaria ananassa</i> Duch.)	increase in dry matter, increase in relative water content (RWC), maintenance of antioxidant activity	Moradtalab et al. 2019
<i>Glomus etunicatum</i> <i>Glomus microaggregatum</i> <i>Glomus intraradices</i> <i>Glomus claroideum</i> <i>Glomus mosseae</i> <i>Glomus geosporum</i>	olive (<i>Olea europaea</i> L.)	increase in relative water content (RWC), increase in turgor pressure, increase in proline content	Sara et al. 2018
<i>Rhizophagus intraradices</i>	maize (<i>Zea mays</i> L.)	increase in dry matter and water use efficiency photosynthesis (WUE)	Zhao et al. 2015

Table 2. Responses of plants in salinity stress to inoculation of different rhizosphere microorganisms

Microorganism	Plant species	Effect	Research author
Plant Growth Promoting Rhizobacteria (PGPR)			
<i>Pseudomonas fluorescens</i>	pistachio tree (<i>Pistacia</i> L.)	deaminase ACC synthesis, production of indole-3-acetic acid (IAA), phosphate solubilization, siderophore production	Azami et al. 2015
<i>Acinetobacter</i> spp. <i>Pseudomonas</i> sp.	barley (<i>Hordeum vulgare</i> L.), oat (<i>Avena sativa</i> L.)	deaminase ACC and indole-3-acetic acid (IAA) synthesis, reducing ethylene production	Chang et al. 2014
<i>Hartmannibacter diazotrophicus</i> E19	barley (<i>Hordeum vulgare</i> L.)	increase in dry matter, deaminase ACC synthesis, reducing ethylene production	Suarez et al. 2015
<i>Pseudomonas putida</i> UW4	rapeseed (<i>Brassica napus</i> L.)	synthesis of ACC deaminase enzyme, modulation of gene expression	Cheng et al. 2011
<i>Haererohalobacter</i> JG-11 <i>Brachybacterium saurashtrense</i> JG-06 <i>Brevibacterium casei</i> JG-08	peanut (<i>Arachis hypogaea</i> L.)	production of abscisic acid (ABA), increased availability of nitrogen (N), phosphorus (P), higher calcium cations (Ca ²⁺) and higher potassium (K ⁺) to sodium (Na ⁺) ratio	Shukla et al. 2012
Plant Growth Promoting Fungi (PGPF)			
<i>Piriformospora indica</i>	aloe (<i>Aloe vera</i> (L.) Burm. f.)	root growth, increase in chlorophyll and flavonoid content	Shama et al. 2016
<i>Cochliobolus</i> sp.	okra (<i>Ablemoschus esculentus</i> (L.) Moench)	plant growth, increase in dry matter, increase in chlorophyll, carotenoids and xanthophylls, increase in relative water content (RWC), increase in soil salinity tolerance with sodium chloride (NaCl)	Bibi et al. 2019
Arbuscular Mycorrhizal Fungi (AMF)			
<i>Glomus deserticola</i>	basil (<i>Ocimum basilicum</i> L.)	reduction of absorption of potassium (K ⁺), phosphorus (P ⁺) and calcium (Ca ²⁺) cations, improved photosynthesis and gas exchange efficiency, increase of chlorophyll content, increase of water use efficiency in photosynthesis (WUE)	Elhindi et al. 2017
<i>Glomus fasciculatum</i>	garlic (<i>Allium sativum</i> L.)	increase in dry matter, increase in photosynthesis and phosphatase activity by increasing nutrient availability	Borde et al. 2010
<i>Glomus mosseae</i> <i>Glomus intraradices</i>	pepper (<i>Capsicum annuum</i> L.)	increase in relative water content (RWC), increase in chlorophyll and carotenoids content	Çekiç et al. 2012

apparatus and starch metabolism in plant cells. The rhizosphere microorganisms induce the processes by which plants are able to inhibit or eliminate the effects of cold stress. These processes include: production of ACC deaminase to minimize the synthesis of ethylene caused by low temperature, increased the nitrogen fixation processes for the plants exposed to frost, synthesis of plant growth regulators (ABA, GA, IAA),

activation of antioxidant enzymes, release of iron chelators (siderophores), and increasing the nutrients uptake (Kushwaha et al. 2020).

According to Turan et al. (2013), the inoculation with PGPR such as *Azospirillum brasilense*, *Bacillus megaterium*, *Bacillus subtilis* and *Raoultella terrigena* minimized the adverse effects of low temperature on barley and wheat seedlings.

Table 3. Responses of plants in temperature stress to inoculation of different rhizosphere microorganisms

Microorganism	Plant species	Effect	Research author
HEAT STRESS (HS)			
Plant Growth Promoting Rhizobacteria (PGPR)			
<i>Pseudomonas lurida</i> M2RH3	wheat (<i>Triticum aestivum</i> L.)	phosphate solubilization, indole-3-acetic acid production, siderophores production	Selvakumar et al. 2011
<i>Pseudomonas aeruginosa</i> 2CpS1	wheat (<i>Triticum aestivum</i> L.)	plant growth, root growth, leaf area index (LAI), increase in chlorophylls content, increase in relative water content (RWC), decrease in cell membrane damage	Meena et al. 2015
<i>Brevibacterium linens</i> RS1	eucalypt (<i>Eucalyptus grandis</i>)	increase in efficiency of the Photosystem II (PSII), increase in CO ₂ assimilation, increase in stomatal conductance	Chatterjee et al. 2019
<i>Bacillus tequilensis</i> SSB07	soybean (<i>Glycine max</i> (L.) Merr.)	shoot growth development of leaves, increase in chlorophyll and carotenoids content, increase in salicylic and jasmonic acid synthesis in the phyllosphere	Kang et al. 2020
Plant Growth Promoting Fungi (PGPF)			
<i>Thermomyces</i> sp.	cucumber (<i>Cucumis sativus</i> L.)	root growth, maintaining the efficiency of the Photosystem II (PSII), increase in water use efficiency (WUE), increase in sugar and protein content	Ali et al. 2018
Arbuscular Mycorrhizal Fungi (AMF)			
<i>Glomus intraradices</i>	asparagus (<i>Asparagus officinalis</i> L.)	shoot growth, increase in root dry matter, increased availability of nitrogen (N), phosphorus (P) and potassium (K), increased activity of antioxidant enzymes (superoxide dismutase, ascorbate peroxidase)	Yeasmin et al. 2019
<i>Rhizophagus intraradices</i> <i>Funneliformis mosseae</i> <i>Funneliformis geosporum</i>	maize (<i>Zea mays</i> L.)	plant growth (shoots, leaves, inflorescences, root system), higher chlorophyll content, maintaining photosynthetic activity	Mathur et al. 2018
<i>Rhizophagus irregularis</i> BEG140 <i>Rhizophagus irregularis</i> <i>Funneliformis mosseae</i> BEG95 <i>Funneliformis geosporum</i> <i>Claroideoglomus claroideum</i>	wheat (<i>Triticum aestivum</i> L.)	plant growth, higher number of grains per spike, increased availability of macro- and microelements, increase in efficiency of the Photosystem II (PSII)	Cabral et al. 2016
COLD STRESS (CS)			
Plant Growth Promoting Rhizobacteria (PGPR)			
<i>Bacillus</i> spp. CJCL2 <i>Bacillus</i> ssp. RJGP41	wheat (<i>Triticum aestivum</i> L.)	increase in proline content, inhibition of lipid peroxidation	Zubair et al. 2019
Arbuscular Mycorrhizal Fungi (AMF)			
<i>Glomus etunicatum</i>	maize (<i>Zea mays</i> L.)	increase in chlorophyll a, b and total chlorophyll content, increase in PS II and photosynthetic efficiency, higher transpiration, increase in stomatal conductance	Zhu et al. 2010b
<i>Glomus mosseae</i>	tomato (<i>Lycopersicon esculentum</i> Mill.)	increase in superoxide dismutase, catalase and ascorbate peroxidase activity, increase in assimilation pigments, sugars and proteins content	Latef i Chaoxing 2011
<i>Rhizophagus intraradices</i>	purging nut (<i>Jatropha curcas</i> L.)	increase in catalase and glutathione peroxidase activity	Pedranzani et al. 2015

Zhu et al. (2010b), Abdel Latef and Chaoxing (2011b), Birhane et al. (2012), Chen et al. (2013) and Liu et al. (2013) stated in their reports that inoculation with AMF increase plant resistance to cold. Supplementary information is shown in the Table 3.

The role of rhizosphere microorganisms in increasing the availability of nutrients in the soil

Nutrient deficiency, even at an asymptomatic level, is an important factor reducing the plants crop (Jewell et al. 2010, Etesami and Adl 2020).

Inoculation with microorganisms such as PGPR and PGPF can affect the availability of nutrients for plants (Zhang et al. 2014, Ma et al. 2015, Damodharan et al. 2018). The processes by which rhizosphere microorganisms directly facilitate the uptake of nutrients or increase their availability include: atmospheric nitrogen fixation, solubilization of sparingly soluble phosphorus and potassium, and synthesis of siderophores (Bhattacharyya and Jha 2012, Hayat et al. 2012, Rana et al. 2012 and Di Salvo et al. 2018).

Atmospheric nitrogen fixation is a process proceeding both non-symbiotic and symbiotic interactions between microorganisms and plants (Sridhar 2012). The nitrogen-fixing microorganisms help to increase the absorption capacity of plants. Roots release exudates, which are processed by bacteria, which then provide plants with assimilable nitrogen for the synthesis of amino acids (Lata et al. 2018). As reported by Kuan et al. (2016), *Rhizobium*, *Pantoea agglomerans*, *Azoarcus* and *Klebsiella pneumoniae* are a group of bacteria that are the most suitable for atmospheric nitrogen fixation in the soil. The rhizosphere microorganisms secrete some organic acids (citric acid, apple acid, succinic acid), which solubilize the phosphorus forms unavailable to plants and transform them into an assimilable inorganic form (Waghunde et al. 2017). Among the types of rhizosphere bacteria, Oteino et al. (2015) distinguish those that promote the process of solubilization (increasing solubility), which include: *Arthrobacter*, *Bacillus*, *Pseudomonas*, *Rhizobium*, *Burkholderia*, *Flavobacterium*, *Rhodococcus* and *Serratia*. Liu et al. (2012) claim that such rhizosphere bacteria as *Acidithiobacillus*, *Bacillus*, *Paenibacillus* and *Pseudomonas* release potassium from potassium compounds into the soil in a form available

to plants. *Pseudomonas putida* produce the iron chelating compounds, i.e. siderophores, and bind them to the rhizosphere, making them available to plants (Rathore 2015). Supplementary information is shown in the Table 4.

The role of rhizosphere microorganisms in the detoxification of heavy metals in the soil

Accumulation of heavy metals is an environmental problem that negatively affect human health, plants, and the soil (Singh et al. 2019). These elements, do not degrade, and are also toxic at low concentrations (Ma et al. 2016a, Ma et al. 2016b).

The interactions of heavy metals with bacteria increase their bioavailability, which can lead to their detoxification or removal from the soil (Mishra et al. 2017). The use of PGPR is a practical, environmentally friendly, and at the same time economical approach to alleviating the stress associated with the high concentration of heavy metals in soil (Upadhyay et al. 2011, Ahemad 2014). Khan and Bano (2016) and Karthik et al. (2017) declared that PGPR increase plant tolerance to heavy metals and reduce their toxicity. According to Khan et al. (2018), PGPR also promote the process of phytoremediation.

As reported by Zhang et al. (2015), bacteria such as: *Proteobacteria*, *Firmicutes* and *Actinobacteria*, eliminate high concentrations of manganese (Mn), lead (Pb) and arsenic (As) from soils. Jing et al. (2014), reported that the bacteria of the *Enterobacter* and *Klebsiella* genera are effective against cadmium, lead and zinc in the soil, through the production of phytohormones (IAA), siderophores, and ACC deaminase synthesis.

According to Kanwal et al. (2015) and Miransari (2017), mycorrhizal fungi, when exerting a positive effect on plant in stress, increase nutrient uptake and biomass production, while reducing the toxicity of metals in plants. Supplementary information is shown in the Table 5.

The role of rhizosphere microorganisms in increasing physiological activity, plant growth and yielding

Hossain et al. (2017) as well as Smith and Read (2008) reported the benefits of the interaction of plants with rhizosphere microorganisms, which include: improved germination, better root and shoot development and growth,

Table 4. Responses of plants in availability of nutrients in the soil to inoculation of different rhizosphere microorganisms

Microorganism	Plant species	Effect	Research author
Plant Growth Promoting Rhizobacteria (PGPR)			
<i>Bacillus</i> M-3 <i>Bacillus</i> OSU-142 <i>Pseudomonas</i> BA-8	strawberry (<i>Fragaria ananassa</i> Duch.)	increase the availability of phosphorus (P), iron (Fe), zinc (Zn), potassium (K) and magnesium (Mg)	Esitken et al. 2010
<i>Pseudomonas aeruginosa</i> BHUJY16 <i>Pseudomonas aeruginosa</i> BHUJY20 <i>Pseudomonas putida</i> BHUJY13 <i>Pseudomonas putida</i> BHUJY23 <i>Pseudomonas fluorescens</i> BHUJY29 <i>Azotobacter chroococcum</i> <i>Azospirillum brasilense</i>	rice (<i>Oryza sativa</i> L.)	increase the availability of nitrogen (N) and phosphorus (P)	Lavakush et al. 2014
<i>Bacillus</i> M3 <i>Bacillus</i> OSU-142 <i>Microbacterium</i> FS01	apple (<i>Malus domestica</i> Borkh.) 'Granny Smith'	increase the availability of nitrogen (N), P (phosphorus), Ca (calcium), potassium (K), zinc (Zn), iron (Fe), manganese (Mn)	Karlidag et al. 2007
<i>Bacillus cereus</i> <i>Pseudomonas</i> sp.	tomato (<i>Lycopersicon esculentum</i> Mill.)	increase the availability of potassium (K)	Etesami et al. 2017
<i>Bacillus amyloliquefaciens</i> IN937a <i>Bacillus pumilus</i> T4	tomato (<i>Lycopersicon esculentum</i> Mill.)	increase in nitrogen (N) availability, phosphate solubilization	Fan et al. 2017
		increase in nitrogen (N) availability	Adesemoye et al. 2010
<i>Bacillus amyloliquefaciens</i> L-S60	cucumber (<i>Cucumis sativus</i> L.)	increase the availability of nitrogen (N), phosphorus (P) and potassium (K)	Qin et al. 2017
<i>Pseudomonas chlororaphis</i> <i>Pseudomonas putida</i>	soybean (<i>Glycine max</i> (L.) Merr.)	phosphate solubilization	Gouda et al. 2018
Plant Growth Promoting Fungi (PGPF)			
<i>Aspergillus tubingensis</i> PSF-4 <i>Aspergillus niger</i> PSF-7	maize (<i>Zea mays</i> L.), wheat (<i>Triticum aestivum</i> L.)	phosphate solubilization	Kaur i Reddy 2016
<i>Aspergillus niger</i> NCIM 563	wheat (<i>Triticum aestivum</i> L.)	phosphate solubilization	Gujar et al. 2013
Arbuscular Mycorrhizal Fungi (AMF)			
<i>Rhizophagus irregularis</i>	barrelclover (<i>Medicago truncatula</i> Gaertn.)	phosphate and zinc solubilization	Nguyen et al. 2019
<i>Glomus mosseae</i> <i>Glomus intraradices</i>	pistachio tree (<i>Pistacia vera</i> L. cv. Qazvini, <i>Pistacia vera</i> L. cv. Badami-Riz-Zarand)	increase the availability of phosphorus (P), potassium (K), zinc (Zn) and manganese (Mn)	Bagheri et al. 2012

morphogenesis, positive impact on flowering, higher photosynthetic rate, and yielding.

PGPR and AMF increase the absorptive surface of roots and nutrients uptake (Leifheit et al. 2015, Sas-Paszt et al. 2011). They can also indirectly affect the intensity of photosynthesis by increasing the stomatal conductance to CO₂ and the efficiency of photochemical reactions. They increase the quantity and quality of yield, especially in the plants growing in stress (Khade and Rodrigues 2009, Karlidag et al. 2013). Seema et al. (2018) demonstrated

that the application of *Bacillus* promotes the assimilation and transpiration in the leaves of strawberry. According to Chen et al. (2017), some of the mycorrhizal fungi genera (*Claroideoglossum*, *Diversispora*, *Funneliformis*, *Rhizophagus*) increase the stomatal conductance and the rate of photosynthesis, in cucumber plants.

According to Hossain et al. (2017), the genera of PGPF such as: *Alternaria*, *Aspergillus*, *Cladosporium*, *Colletotrichum*, *Exophiala*, *Fusarium*, *Penicillium*, *Phoma*, *Phomopsis*, *Rhizoctonia*,

Table 5. Responses of plants exposed to heavy metal accumulation in the soil to inoculation with different rhizosphere microorganisms

Microorganism	Plant species	Effect	Research author
Plant Growth Promoting Rhizobacteria (PGPR)			
<i>Bacillus cereus</i> <i>Pseudomonas moraviensis</i>	wheat (<i>Triticum aestivum</i> L.)	reduction of cadmium (Cd), cobalt (Co), chromium (Cr), copper (Cu) and manganese (Mn) in the soil	Hassan et al. 2016
<i>Planomicrobium chinense</i> P1 <i>Bacillus cereus</i> P2	sunflower (<i>Helianthus annuus</i> L.)	reduction of cadmium (Cd), lead (Pb) and nickel (Ni) in the soil	Khan et al. 2018
<i>Rhizobium leguminosarum</i> (M5) <i>Bacillus simplex</i> <i>Luteibacter</i> sp. <i>Variovorax</i> sp.	grass pea (<i>Lathyrus sativus</i> L.)	reduction of cadmium (Cd) and lead (Pb) in the soil	Abdelkrim et al. 2020
<i>Rhizobium leguminosarum</i> (M5) <i>Pseudomonas fluorescens</i> (K23) <i>Luteibacter</i> sp. <i>Variovorax</i> sp.			
<i>Bacillus thuringiensis</i> GDB-1	<i>Alnus firma</i> Siebold & Zucc	reduction of arsenic (As), lead (Pb), nickel (Ni), zinc (Zn), copper (Cu) in the soil	Babu et al. 2013
<i>Thiobacillus thiooxidans</i> <i>Pseudomonas putida</i>	gladiolus, sword lily (<i>Gladiolus grandiflorus</i> L.)	reduction of cadmium (Cd) and lead (Pb) in the soil	Mani et al. 2016
<i>Bradyrhizobium japonicum</i>	lettuce (<i>Lactuca sativa</i> L.)	reduction of copper (Cu) and nickel (Ni) in the soil	Seneviratne et al. 2016
<i>Bacillus pumilus</i> E2S2	<i>Sedum plumbizincicola</i> X.H.Guo & S.B.Zhou ex L.H.Wu	reduction of cadmium (Cd) and zinc (Zn) in the soil	Ma et al. 2015
Arbuscular Mycorrhizal Fungi (AMF)			
<i>Glomus mosseae</i> BEG167	maize (<i>Zea mays</i> L.)	increase tolerance to cadmium (Cd) and zinc (Zn) in plants	Shen et al. 2006
<i>Glomus etunicatum</i> <i>Glomus macrocarpum</i> <i>Gigaspora margarita</i>	Moluccan albizia (<i>Falcataria moluccana</i> Miq.)	lower soil pH, plant growth (shoots, roots), increase in dry matter, increase in soil organic carbon (C), reduction in soil copper (Cu)	Rollon et al. 2017
<i>Glomus intraradices</i>	tobacco (<i>Nicotiana tabacum</i> L.)	de-accumulation of cadmium (Cd) in the soil	Janoušková and Pavlíková 2010
	alfalfa (<i>Medicago sativa</i> L.)	de-accumulation of cadmium (Cd) in the soil	Wang et al. 2012

Trichoderma, contribute to the acceleration of plant growth. Chirino-Valle et al. (2016) found the impact of inoculation with *Trichoderma* fungi on the growth of the giant miscanthus (*Miscanthus × giganteus*). According to Vázquez-de-Aldana et al. (2013), Hossain et al. (2014) and Islam et al. (2014b), many PGPF genera also stimulate root system development. Supplementary information is shown in the Table 6.

The role of rhizosphere microorganisms in pathogen elimination

According to Etesami and Maheshwari (2018), Berendsen et al. (2012) and also Pieterse et al. (2014) PGPR, PGPF and AMF can

protect plants against pathogenic microorganisms by activation systemic resistance in plants (ISR). ISR can be induced by fungi PGPF such as *Fusarium*, *Penicillium*, *Phytophthora*, *Pythium*, *Trichoderma* and also AMF such as *Funneliformis*, *Glomus*, and *Rhizophagus* (Bent 2006). Induction of this resistance eliminates the harmful effects of bacteria, fungi, viruses and nematodes on plants (Fontenelle et al. 2011, Elsharkawy et al. 2012, Hossain and Sultana 2015, Vu et al. 2006). Lee et al. (2015), in their study on the induction of ISR in ginseng infected with *Phytophthora cactorum*, showed that inoculation with *Bacillus amyloliquefaciens* HK34 induced ISR. Supplementary information is shown in the Table 7.

Table 6. The role of different rhizosphere microorganisms in physiological activity, plant growth and yielding

Microorganism	Plant species	Effect	Research author
Plant Growth Promoting Rhizobacteria (PGPR)			
<i>Bacillus</i> M3 <i>Bacillus</i> OSU-142 <i>Microbacterium</i> FS01	apple (<i>Malus domestica</i> Borkh.) 'Granny Smith'	increase in yield, increase in fruit weight, increase in shoot length and thickness	Karlidag et al. 2007
<i>Bacillus amyloliquefaciens</i> IT45	strawberry (<i>Fragaria ananassa</i> Duch.)	increase chlorophyll a and total chlorophylls, rate of transpiration and CO ₂ concentration in the intercellular spaces in the leaves, increase chlorophyll fluorescence	Mikiciuk et al. 2019b
<i>Pseudomonas putida</i> R-168 <i>Pseudomonas fluorescens</i> R-93 <i>Pseudomonas fluorescens</i> DSM 50090 <i>Pseudomonas putida</i> DSM291 <i>Azospirillum lipoferum</i> DSM 1691 <i>Azospirillum brasilense</i> DSM 1690	maize (<i>Zea mays</i> L.)	better seed germination, dry matter and plant growth	Gholami et al. 2009
<i>Azospirillum</i> spp. <i>Azoarcus</i> spp. <i>Azorhizobium</i> spp.	wheat (<i>Triticum aestivum</i> L.)	increase in the root system, increase in nitrogen (N) availability for plants	Dal Cortivo et al. 2017
Plant Growth Promoting Fungi (PGPF)			
<i>Trichoderma atroviride</i>	Giant Miscanthus (<i>Miscanthus × giganteus</i>)	higher shoot length	Chirino-Valle et al. 2016
<i>Cladosporium</i> sp. MH-6	<i>Suaeda japonica</i> Makino	increase in shoot length, fresh and dry matter	Hamayun et al. 2010
<i>Epichloë festucae</i>	red fescue (<i>Festuca rubra</i> L.)	increase in root mass	Vázquez-de-Aldana et al. 2013
<i>Penicillium viridicatum</i> GP15-1	cucumber (<i>Cucumis sativus</i> L.)	greater root fresh mass and root dry mass, higher root length	Hossain et al. 2014
<i>Fusarium</i> spp. PPF1	Malabar spinach, Indian spinach (<i>Basella alba</i> L.)	greater root fresh mass and root dry mass, higher root length	Islam et al. 2014b
<i>Penicillium expansum</i> <i>Penicillium bilaii</i> <i>Penicillium implicatum</i> <i>Penicillium oxalicum</i> <i>Penicillium verrucosum</i> <i>Penicillium simplicissimum</i> <i>Penicillium citrinum</i>	tomato (<i>Lycopersicon esculentum</i> Mill.)	better seed germination, plant growth (shoot and root system)	Mushtaq et al. 2012
<i>Penicillium chrysogenum</i> <i>Phoma</i> sp. <i>Trichoderma koningi</i>	opuntia (<i>Opuntia streptacantha</i> Lem.)	seed dormancy interruption	Delgado-Sanchez et al. 2011
<i>Penicillium chrysogenum</i> <i>Penicillium aurantiogriseum</i> <i>Saccharomyces cerevisiae</i>	thale cress (<i>Arabidopsis thaliana</i> (L.) Heynh.)	flowering induction	Sánchez-López et al. 2016
<i>Piriformospora indica</i>	Indian Coleus (<i>Coleus forskohlii</i> Briq)	speeding up flowering, increase flowering intensity	Das et al. 2012
<i>Trichoderma harzianum</i> T-3 <i>Rhizoctonia solani</i> RS10	pea (<i>Pisum sativum</i> L.)	increase yielding	Akhter et al. 2015
<i>Pochonia chlamydosporia</i>	tomato (<i>Lycopersicon esculentum</i> Mill.)	higher fruit number and weight	Zavala-Gonzalez et al. 2015
Arbuscular Mycorrhizal Fungi (AMF)			
<i>Rhizophagus irregularis</i> <i>Glomus mosseae</i> <i>Claroideoglomus etunicatum</i>	grapevine (<i>Vitis vinifera</i> L.) 'Pinot Noir', 'Regent', 'Rondo'	increase in CO ₂ assimilation, transpiration and stomatal conductance	Mikiciuk et al. 2019a
<i>Rhizophagus irregularis</i> CD1	cotton (<i>Gossypium hirsutum</i> L.)	increase yielding, improving fruit quality	Gao et al. 2020
<i>Rhizophagus irregularis</i> , <i>Funneliformis mosseae</i> , <i>Claroideoglomus etunicatum</i> <i>Rhizophagus intraradices</i>	strawberry (<i>Fragaria ananassa</i> Duch.)	increase chlorophyll a and total chlorophylls, rate of transpiration and CO ₂ concentration in the intercellular spaces in the leaves, increase chlorophyll fluorescence	Mikiciuk et al. 2019b

Table 7. Responses of plants exposed to pathogens to inoculation with different rhizosphere microorganisms

Microorganism	Plant species	Pathogen	Effect	Research author
Plant Growth Promoting Rhizobacteria (PGPR)				
<i>Paenibacillus</i> P16	cabbage (<i>Brassica oleracea</i> var. <i>capitata</i> L.)	<i>Xanthomonas campestris</i> pv. <i>campestris</i> (Xcc)	reduce severity of black rot in cabbage.	Ghazalibiglar et al. 2016
<i>Brevibacterium iodinum</i> KUDC1716	pepper (<i>Capsicum annuum</i> L.)	<i>Stemphylium lycopersici</i>	reduce severity of gray leaf spot in pepper	Son et al. 2014
<i>Bacillus pumilus</i> INR7 <i>Bacillus pumilus</i> SE34 <i>Bacillus pumilus</i> T4 <i>Bacillus amyloliquefaciens</i> IN937a <i>Bacillus subtilis</i> IN937b <i>Bacillus subtilis</i> GB03 <i>Brevibacillus brevis</i> IPC11	rice (<i>Oryza sativa</i> L.)	<i>Xanthomonas oryzae</i> pv. <i>oryzae</i> (Xoo)	reduce severity of bacterial leaf blight in rice	Chithrashree et al. 2011
<i>Bacillus amyloliquefaciens</i> HK34	ginseng (<i>Panax ginseng</i> C.A. Meyer)	<i>Phytophthora cactorum</i>	identification of marker genes (PgPR5, PgPR10 i PgCAT), induction of ISR	Lee et al. 2015
Plant Growth Promoting Fungi (PGPF)				
<i>Meyerozyma guilliermondii</i> TA-2	cabbage (<i>Brassica oleracea</i> var. <i>capitata</i> L.)	<i>Alternaria brassicicola</i>	reduce severity of black rot in cabbage	Elsharkawy et al. 2015
	tomato (<i>Lycopersicon</i> <i>esculentum</i> Mill.)	<i>Ralstonia solanacearum</i>	reduce severity of tomato bacterial wilt	
	rice (<i>Oryza sativa</i> L.)	<i>Magnaporthe oryzae</i>	reduce severity of rice blast	
<i>Fusarium</i> spp. UPM31P1	tomato (<i>Lycopersicon</i> <i>esculentum</i> Mill.)	<i>Fusarium oxysporum</i> f. sp. <i>cubense</i> race 4	reduce severity of fusarium wilt in tomato	Ting et al. 2010
<i>Penicillium</i> sp. GP15-1	cucumber (<i>Cucumis</i> <i>sativus</i> L.)	<i>Colletotrichum orbiculare</i>	reduction number of lesions (anthracnose) on leaves	Hossain et al. 2014
<i>Ampelomyces</i> sp. <i>Cladosporium</i> sp.	thale cress (<i>Arabidopsis</i> <i>thaliana</i> (L.) Heynh.)	<i>Pseudomonas syringae</i> pv. <i>tomato</i> DC3000	reduce severity of bacterial speck of tomato, pathogen proliferation	Naznin et al. 2014
<i>Talaromyces wortmannii</i> FS2	komatsuna, mustard spinach (<i>Brassica</i> <i>campestris</i> var. <i>perviridis</i>)	<i>Colletotrichum</i> <i>higginsianum</i>	produce β -caryophyllene, enhance resistance/ tolerance	Yamagiwa et al. 2011
Arbuscular Mycorrhizal Fungi (AMF)				
<i>Funneliformis mosseae</i> <i>Rhizophagus irregularis</i>	paradise apple (<i>Malus pumila</i> Mill.)	<i>Neonectria ditissima</i>	increase resistance to <i>Neonectria</i> <i>ditissima</i>	Berdeni et al. 2018

CONCLUSIONS

The plant growth promoting microorganisms are important to the rhizosphere and can improve the growth and development of plants. PGPM can support the human activity in protecting plants from stress factors in agricultural and horticultural crops. Furthermore, they contribute to the availability of nutrients and protection against soil pathogens, and have an significant

role in phytoremediation and soil fertility improvement. This issue is extremely important and requires further research on the possibilities of using microorganisms in global plant production in different ecosystems. The extension of the research should be based on a thorough analysis of the plant–microorganism–stress factor–soil interactions. Understanding the interrelationships between these factors is important for improving the rational application of PGPM in plant crops.

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