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, Alpharhizobium, Arthrobacter, Azorhizobium, Azospirillum, Bacillus, Bradyrhizobium, Burkholderia, Enterobacter, Erwinia, Flavobacterium, Frankia, Melorhizobium, 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 *Glomera mycota* 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, Yoooyongwech 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 *Acephobacter*, *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 *Rhizopagus 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)** | | | |
| *Pseudomonas libanensis* TR1 | *Brassica oleracea* Coss. | plant growth, increase in leaf water content (LWC), increase in chlorophyll content | Ma et al. 2016a |
| *Pseudomonas reactans* Ph3R3 | *maize* (Zea mays L.) | increase in relative water content (RWC), increase in protein and sugar content, increase in proline content | Naseem and Bano 2014 |
| *Proteus penneri* Pp1 | *Brassica oxyrrhina* Coss. | increase in plant growth, increase in leaf water content (LWC), increase in chlorophyll content | Ma et al. 2016a |
| *Pseudomonas aeruginosa* (Pa2) | *maize* (Zea mays L.) | increase in relative water content (RWC), increase in chlorophyll and proline content | Zhang et al. 2016 |
| *Alcaligenes faecalis* (AF3) | *maize* (Zea mays L.) | increase in relative water content (RWC), increase in chlorophyll and proline content | Zhang et al. 2016 |
| *Trichoderma longibrachiatum* | *thale cress* (Arabidopsis thaliana (L.) Heynh.) | increase in plant yielding, increase in relative water content (RWC), increase in proline content | Cohen et al. 2015 |
| *Azospirillum brasilense* Sp 245 | *maize* (Zea mays L.) | increase in plant growth, increase in leaf water content (LWC), increase in chlorophyll content | Ma et al. 2016a |
| *Pseudomonas entomophila* BV-P13 | *maize* (Zea mays L.) | increase in plant yielding, increase in relative water content (RWC), increase in proline content | Vardharajula et al. 2010 |
| *Proteus penneri* Pp1 | *maize* (Zea mays L.) | increase in relative water content (RWC), increase in chlorophyll and proline content | Zhang et al. 2016 |
| *Pseudomonas stutzeri* GRFAP-P45 | *maize* (Zea mays L.) | increase in relative water content (RWC), increase in chlorophyll and proline content | Zhang et al. 2016 |
| *Pseudomonas syringae* GRFHYTP5 | *maize* (Zea mays L.) | increase in relative water content (RWC), increase in chlorophyll and proline content | Zhang et al. 2016 |
| *Pseudomonas monteilii* WAPP53 | *maize* (Zea mays L.) | increase in relative water content (RWC), increase in chlorophyll and proline content | Zhang et al. 2016 |
| *Bacillus cereus* AR156 | *cucumber* (Cucumis sativus L.) | activation of Induced Systemic Resistance (ISR), maintain photosynthetic performance, vigour and antioxidant activity | Wang et al. 2012 |
| *Bacillus subtilis* SM21 | *cucumber* (Cucumis sativus L.) | activation of Induced Systemic Resistance (ISR), maintain photosynthetic performance, vigour and antioxidant activity | Wang et al. 2012 |
| *Serratia sp.* XY21 | *cucumber* (Cucumis sativus L.) | activation of Induced Systemic Resistance (ISR), maintain photosynthetic performance, vigour and antioxidant activity | Wang et al. 2012 |
| *Pseudomonas aeruginosa* GGRJ21 | *maize* (Zea mays L.) | increase in proline, sugars and free amino acids content | Vardharajula et al. 2010 |
| **Plant Growth Promoting Fungi (PGPF)** | | | |
| *Trichoderma atroviride* ID20G | *maize* (Zea mays 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 |
| *Exophiala sp.* LHL08 | *cucumber* (Cucumis sativus L.) | abscisic acid (ABA), salicylic acid (SA) and gibberellin (GA) induction | Khan et al. 2011a |
| **Arbuscular Mycorrhizal Fungi (AMF)** | | | |
| *Rhizophagus irregularis* | *lettuce* (Lactuca sativa L.), tomato (Lycopersicon esculentum Mill.) | plant growth, indole-3-acetic acid production, increase in Photosystem II (PSII) performance | Ruiz-Lozano et al. 2015 |
| *Glomus intraradices* | *sweet potato* (Ipomoea batatas (L.) Por) | increase in efficiency of Photosystem II (PSII), increase in chlorophyll, proline and sugars content | Yooyongwech et al. 2016 |
| *Acaulospora* sp. | *strawberry* (Fragaria ananassa Duch.) | increase in dry matter, increase in relative water content (RWC), maintenance of antioxidant activity | Moradtalab et al. 2019 |
| *Rhizophagus clarus* | *olive* (Olea europaea L.) | increase in relative water content (RWC), increase in turgor pressure, increase in proline content | Sara et al. 2018 |
| *Glomus etunicatum* | *maize* (Zea mays 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)** | | | |
| *Pseudomonas fluorescens*     | pistachio tree (Pistacia L.) | deaminase ACC synthesis, production of indole-3-acetic acid (IAA), phosphate solubilization, siderophore production | Azami et al. 2015 |
| *Acinetobacter spp.*          | barley (Hordeum vulgare L.), oat (Avena sativa L.) | deaminase ACC and indole-3-acetic acid (IAA) synthesis, reducing ethylene production | Chang et al. 2014 |
| *Hartmannibacter diazotrophicus* E19 | barley (Hordeum vulgare L.) | increase in dry matter, deaminase ACC synthesis, reducing ethylene production | Suarez et al. 2015 |
| *Pseudomonas putida UW4*      | rapeseed (Brassica napus L.) | synthesis of ACC deaminase enzyme, modulation of gene expression | Cheng et al. 2011 |
| *Haererohalobacter JG-11*     | peanut (Arachis hypogaea L.) | production of abscisic acid (ABA), increased availability of nitrogen (N), phosphorus (P), higher calcium cations (Ca2+) and higher potassium (K+) to sodium (Na+) ratio | Shukla et al. 2012 |
| **Plant Growth Promoting Fungi (PGPF)** | | | |
| *Piriformospora indica*       | aloe (Aloe vera (L.) Burm. f.) | root growth, increase in chlorophyll and flavonoid content | Sharma et al. 2016 |
| *Cochliobolus sp.*            | okra (Abelmoschus esculentus (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)** | | | |
| *Glomus deserticola*          | basil (Ocimum basilicum L.) | reduction of absorption of potassium (K+), phosphorus (P+) and calcium (Ca2+) cations, improved photosynthesis and gas exchange efficiency, increase of chlorophyll content, increase of water use efficiency in photosynthesis (WUE) | Elhindi et al. 2017 |
| *Glomus fasciculatum*         | garlic (Allium sativum L.) | increase in dry matter, increase in photosynthesis and phosphatase activity by increasing nutrient availability | Borde et al. 2010 |
| *Glomus mosseae*              | pepper (Capsicum annuum L.) | increase in relative water content (RWC), increase in chlorophyll and carotenoids content | Çekiç et al. 2012 |

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)** |                          |                                              |                             |
| *Pseudomonas lurida* M2RH3           | wheat (Triticum aestivum L.) | phosphate solubilization, indole-3-acetic acid production, siderophores production         | Selvakumar et al. 2011      |
| *Pseudomonas aeruginosa* 2CpS1       | wheat (Triticum aestivum 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           |
| *Brevibacterium linens* RS1          | eucalypt (Eucalyptus grandis) | increase in efficiency of the Photosystem II (PSII), increase in CO$_2$ assimilation, increase in stomatal conductance | Chatterjee et al. 2019      |
| *Bacillus tequilensis* SSB07         | soybean (Glycine max (L.) Merr.) | shoot growth development of leaves, increase in chlorophyll and carotenoids content, increase in salicylic and jasmonic acid synthesis in the phylosphere | Kang et al. 2020            |
| **Plant Growth Promoting Fungi (PGPF)** |                          |                                              |                             |
| *Thermomyces* sp.                    | cucumber (Cucumis sativus 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)** |                          |                                              |                             |
| *Glomus intraradices*                | asparagus (Asparagus officinalis L.) | shoot growth, increase in root dry matter, increased availability of nitrogen (N), phosphorous (P) and potassium (K), increased activity of antioxidant enzymes (superoxide dismutase, ascorbate peroxidase) | Yeasmin et al. 2019         |
| *Rhizophagus intraradices*           | maize (Zea mays L.)       | plant growth (shoots, leaves, inflorescences, root system), higher chlorophyll content, maintaining photosynthetic activity | Mathur et al. 2018          |
| *Funneliformis mosseae* *Funneliformis geosporum* |                          |                                              |                             |
| *Rhizophagus irregularis* BEG140     | wheat (Triticum aestivum 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)** |                          |                                              |                             |
| *Bacillus* spp. CJCL2                | wheat (Triticum aestivum L.) | increase in proline content, inhibition of lipid peroxidation                                | Zubair et al. 2019          |
| *Bacillus* spp. RJGP41               |                          |                                              |                             |
| **Arbuscular Mycorrhizal Fungi (AMF)** |                          |                                              |                             |
| *Glomus etunicatum*                  | maize (Zea mays 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             |
| *Glomus mosseae*                     | tomato (Lycopersicon esculentum Mill.) | increase in superoxide dismutase, catalase and ascorbate peroxidase activity, increase in assimilation pigments, sugars and proteins content | Latef i Chaoxing 2011       |
| *Rhizophagus intraradices*           | purging nut (Jatropha curcas L.) | increase in catalase and glutathione peroxidase activity                                    | Pedrazani et al. 2015       |
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’ growth and development (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*, *Azorarcus* 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 *Acidothiobacillus, 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 3.

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

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 (Claroideoglomus, 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) |                                    |                                                                        |                             |
| *Bacillus cereus*                  | wheat (Triticum aestivum L.)       | reduction of cadmium (Cd), cobalt (Co), chromium (Cr), copper (Cu) and manganese (Mn) in the soil | Hassan et al. 2016          |
| *Pseudomonas moraviensis*          |                                    |                                                                        |                             |
| Planomicrobiurn chinenae P1        | sunflower (Helianthus annus L.)    | reduction of cadmium (Cd), lead (Pb) and nickel (Ni) in the soil       | Khan et al. 2018            |
| *Bacillus cereus P2*               |                                    |                                                                        |                             |
| *Rhizobium leguminosarum* (M5)     | *Bacillus simplex*                 |                                                                        |                             |
| *Luteibacter sp.*                  | *Variovorax sp.*                   |                                                                        |                             |
| *Planomicrobiurn chinenae P1 M5*   | *Bacillus simplex*                 |                                                                        |                             |
| *Luteibacter sp.*                  | *Variovorax sp.*                   |                                                                        |                             |
| *Rhizobium leguminosarum* (M5)     | *Pseudomonas fluorescens* (K23)    |                                                                        |                             |
| *Luteibacter sp.*                  | *Variovorax sp.*                   |                                                                        |                             |
| *Bacillus thuringiensis* GDB-1     | *Aitlin firma* Siebold & Zucc      | reduction of arsenic (As), lead (Pb), nickel (Ni), zinc (Zn), copper (Cu) in the soil | Babu et al. 2013            |
| *Thiobacillus thiooxidans*         | *Pseudomonas putida*               | reduction of cadmium (Cd) and lead (Pb) in the soil                    | Mani et al. 2016            |
| *Pseudomonas putida*               | *Gladiolus grandiflacus*          | reduction of copper (Cu) and nickel (Ni) in the soil                    | Seneviratne et al. 2016     |
| *Bradyrhizobium japonicum*         | *Aitlin firma* Siebold & Zucc      | reduction of arsenic (As), lead (Pb), nickel (Ni), zinc (Zn), copper (Cu) in the soil | Babu et al. 2013            |
| *Bacillus pumilus E2S2*            | *Sedum plumbeizincicola*           | reduction of cadmium (Cd) and lead (Pb) in the soil                    | Ma et al. 2015              |
| *Bradyrhizobium japonicum*         | *Aitlin firma* Siebold & Zucc      | reduction of arsenic (As), lead (Pb), nickel (Ni), zinc (Zn), copper (Cu) in the soil | Babu et al. 2013            |
| *Arbuscular Mycorrhizal Fungi (AMF)* |                                    |                                                                        |                             |
| *Glomus mossea* BE167              | maize (Zea mays L.)                | increase tolerance to cadmium (Cd) and zinc (Zn) in plants             | Shen et al. 2006            |
| *Glomus etunicatum*                |                                    |                                                                        |                             |
| *Glomus macrocarpum*               |                                    |                                                                        |                             |
| *Gigaspora margarita*              |                                    |                                                                        |                             |
| *Glomus intraradices*              | tobacco (Nicotiana tabacum L.)     | de-accumulation of cadmium (Cd) in the soil                            | Janoušková and Pavlíková 2010 |
| *Glomus mossea* BE167              | alfalfa (Medicago sativa L.)       | de-accumulation of cadmium (Cd) in the soil                            | Wang et al. 2012            |
| *Glomus etunicatum*                |                                    |                                                                        |                             |
| *Glomus macrocarpum*               |                                    |                                                                        |                             |
| *Gigaspora margarita*              |                                    |                                                                        |                             |
| *Glomus intraradices*              | tobacco (Nicotiana tabacum L.)     | de-accumulation of cadmium (Cd) in the soil                            | Janoušková and Pavlíková 2010 |
| *Glomus mossea* BE167              | alfalfa (Medicago sativa 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), Hosain 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, Hosain and Sul tana 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)** | | | |
| *Bacillus* M3<br>*Bacillus* OSU-142<br>*Microbacterium* FS01 | apple *(Malus domestica Borkh.) ‘Granny Smith’* | increase in yield, increase in fruit weight, increase in shoot length and thickness | Karlidag et al. 2007 |
| *Bacillus* amylovorum IT45 | strawberry *(Fragaria ananassa Duch.)* | increase chlorophyll a and total chlorophylls, rate of transpiration and CO₂ concentration in the intercellular spaces in the leaves, increase chlorophyll fluorescence | Mikiciuk et al. 2019b |
| *Pseudomonas* putida R-168<br>*Pseudomonas* fluorescens R-93<br>*Pseudomonas* fluorescens DSM 50090<br>*Azospirillum* lipoforum DSM 1691<br>*Azospirillum* brasiliense DSM 1690 | maize *(Zea mays L.)* | better seed germination, dry matter and plant growth | Gholami et al. 2009 |
| *Azospirillum* spp., *Azoarcus* spp., *Azorhizobium* spp. | wheat *(Triticum aestivum L.)* | increase in the root system, increase in nitrogen (N) availability for plants | Dal Cortivo et al. 2017 |
| **Plant Growth Promoting Fungi (PGPF)** | | | |
| *Trichoderma* atroviride | Giant Miscanthus *(Miscanthus × giganteus)* | higher shoot length | Chirino-Valle et al. 2016 |
| *Cladosporium* sp. MH-6 | *Suada japonica* Makino | increase in shoot length, fresh and dry matter | Hamayun et al. 2010 |
| *Epichloë* fastueae | red fescue *(Festuca rubra L.)* | increase in root mass | Vázquez-de-Aldana et al. 2013 |
| *Penicillium* viridicatum GP15-1 | cucumber *(Cucumis sativus L.)* | greater root fresh mass and root dry mass, higher root length | Hossain et al. 2014 |
| *Fusarium* spp. PPF1 | Malabar spinach, *Indian spinach* *(Basella alba L.)* | greater root fresh mass and root dry mass, higher root length | Islam et al. 2014b |
| *Penicillium* expansum<br>*Penicillium* bilai<br>*Penicillium* implicatum<br>*Penicillium* oxalicum<br>*Penicillium* verrucosum<br>*Penicillium* simplicissimum<br>*Penicillium* citrinum | *Tomato* *(Lycopersicon esculentum Mill.)* | better seed germination, plant growth (shoot and root system) | Mushtaq et al. 2012 |
| *Penicillium* chrysogenum<br>*Phoma* sp., *Trichoderma* koningi | opuntia *(Opuntia streptacantha Lem.)* | seed dormancy interruption | Delgado-Sanchez et al. 2011 |
| *Penicillium* chrysogenum<br>*Penicillium* aurantiogriseum<br>*Saccharomyces* cerevisiae | thale cress *(Arabidopsis thaliana (L.) Heynh.)* | flowering induction | Sánchez-López et al. 2016 |
| *Pirimorforpora* indica | Indian Coleus *(Coleus forskohlii Briq)* | speeding up flowering, increase flowering intensity | Das et al. 2012 |
| *Trichoderma* harzianum T-3<br>*Rhizoctonia* solani RS10 | pea *(Pisum sativum L.)* | increase yielding | Akhter et al. 2015 |
| *Pochonia* chlamydospora | tomato *(Lycopersicon esculentum Mill.)* | higher fruit numner and weight | Zavala-Gonzalez et al. 2015 |
| **Arbuscular Mycorrhizal Fungi (AMF)** | | | |
| *Rhizophagus* irregularis<br>*Glomus* mosseae<br>*Claroideoglomus* etunicatum | grapevine *(Vitis vinifera L.)* ‘Pinot Noir’, ‘Regent’, ‘Rondo’ | increase in CO₂ assimilation, transpiration and stomatal conductance | Mikiciuk et al. 2019a |
| *Rhizophagus* irregularis CD1 | cotton *(Gossypium hirsutum L.)* | increase yielding, improving fruit quality | Gao et al. 2020 |
| *Rhizophagus* irregularis, *Funnelliformis* mosseae, *Claroideoglomus* etunicatum *Rhizophagus* intraradices | strawberry *(Fragaria ananassa Duch.)* | increase chlorophyll a and total chlorophylls, rate of transpiration and CO₂ 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)** |                                |                                               |                                             |                              |
| *Paenibacillus* P16           | cabbage (Brassica oleracea var. capitata L.) | *Xanthomonas campestris pv. campestris* (Xcc) | reduce severity of black rot in cabbage.   | Ghazalibiglar et al. 2016    |
| *Brevibacterium iodinum* KUDEC1716 | pepper (Capsicum annuum L.) | *Stemphylium lycopersici*                     | reduce severity of gray leaf spot in pepper| Son et al. 2014              |
| *Bacillus* pumilus INR7        | *rice* (Oryza sativa L.)      | *Xanthomonas oryzae pv. oryzae* (Xoo)         | reduce severity of bacterial leaf blight in rice | Chithrashree et al. 2011     |
| *Bacillus* pumilus SE34        |                                |                                               |                                             |                              |
| *Bacillus* pumilus T4          |                                |                                               |                                             |                              |
| *Bacillus* amylophiliquefaciens IN937b |                                |                                               |                                             |                              |
| *Bacillus* subtilis GB03       |                                |                                               |                                             |                              |
| *Brevibacillus brevis* IPC11   |                                |                                               |                                             |                              |
| *Bacillus* amylophiliquefaciens HK34 | ginseng (Panax ginseng C.A. Meyer) | *Phytophthora cactorum*                       | identification of marker genes (PgPR5, PgPR10 i PgCAT), induction of ISR | Lee et al. 2015              |
| **Plant Growth Promoting Fungi (PGPF)** |                                |                                               |                                             |                              |
| *Meyerozyma guilliermondii* TA-2 | cabbage (Brassica oleracea var. capitata L.) | *Alternaria brassicicola*                     | reduce severity of black rot in cabbage    |                              |
|                                | tomato (Lycopersicon esculentum Mill.) | *Ralstonia solanacearum*                      | reduce severity of tomato bacterial wilt   | Elsharkawy et al. 2015       |
|                                | *rice* (Oryza sativa L.)       | *Magnaporthe oryzae*                         | reduce severity of rice blast              |                              |
| *Fusarium* spp. UPM31P1        | tomato (Lycopersicon esculentum Mill.) | *Fusarium oxysporum* f. sp. cubense race 4    | reduce severity of fusarium wilt in tomato | Ting et al. 2010             |
| *Penicillium* sp. GP15-1       | cucumber (Cucumis sativus L.)  | *Colletotrichum orbiculare*                   | reduction number of lesions (anthracnose) on leaves | Hossain et al. 2014         |
| *Ampelomyces* sp.               | thale cress (Arabidopsis thaliana (L.) Heyn.) | *Pseudomonas syringae pv. tomato* DC3000       | reduce severity of bacterial speck of tomato, pathogen proliferation | Naznin et al. 2014          |
| *Cladosporium* sp.             |                                |                                               |                                             |                              |
| *Talaromyces wortmannii* FS2   | komatsuna, mustard spinach (Brassica campestris var. perviridis) | *Colletotrichum higginsianum*                 | produce β-caryophyllene, enhance resistance/tolerance | Yamagiwa et al. 2011         |
| **Arbuscular Mycorrhizal Fungi (AMF)** |                                |                                               |                                             |                              |
| *Funneliformis mosseae*        | *paradise apple* (Malus pumila Mill.) | *Neonectria ditissima*                        | increase resistance to *Neonectria ditissima* | 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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