COMPREHENSIVE REVIEW ON PLANT GROWTH PROMOTING RHIZOBACTERIA IN RELEVANCE TO ABIOTIC STRESS TOLERANCE OF PLANTS


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Abstract. The rhizosphere represents an intricate microenvironment, consisting of a complex network involving soil, root and soil microbes. Conditions in the rhizosphere exert a direct influence on the growth and yield of crops. The unregulated and widespread application of synthetic fertilizers has emerged as a grave concern for the sustainability of agriculture and the equilibrium of ecosystems. These chemical substances accumulate within the soil, leach into water sources and release into the atmosphere, persisting for decades and posing a substantial threat to the overall ecosystem. This issue is of significant concern, necessitating a potential solution that can only be realized through the involvement of microorganisms and organic amendments. Plant growth promoting rhizobacteria (PGPR) has assumed a pivotal role in addressing this concern. The established role of microorganisms in enhancing plant growth, managing nutrients and exerting biocontrol is well-documented. PGPR, present in the rhizosphere, has the capacity to transform numerous nutrients that are initially inaccessible to plants into forms that can be readily utilized. Additionally, PGPR synthesize plant hormones, secondary metabolites, antibiotics, stress-relieving compounds, chelating agents, and signaling molecules, enabling interactions with both beneficial and pathogenic organisms within the rhizosphere. Moreover, PGPR is involved in the improvement of soil physical properties, chemical properties and overall functioning that offers direct or indirect benefits to crop growth.

Keywords: rhizosphere, tolerance, microbiome, PGPR and abiotic stress

Introduction

In recent times, agriculture has been confronting significant challenges arising from both biological and environmental factors. Meeting the food needs of the expanding global population, which is projected to reach an estimated 9.5-10 billion by 2050 from the current 8 billion, is becoming a critical issue worldwide. The population growth-driven pressure on agriculture has led to the widespread adoption of high-yield crop varieties, the excessive use of chemical fertilizers, intensive cultivation methods, and the increased application of pesticides to maximize crop production. Unfortunately, these practices have resulted in adverse consequences such as the release of greenhouse
gases, water pollution, and soil contamination, all of which have emerged as recent issues in agriculture (Karunakaran and Behera, 2016 and Dhanushkodi et al., 2023). Given these factors, the agricultural system is facing huge stress related to ensuring food security, addressing the challenges of climate change, and improving soil health (Lal, 2015 and Dhanushkodi et al., 2021).

This review will specifically explore the concept of rhizosphere engineering (RE) with a focus on the advantages it offers to plants, nutrient absorption, and ecological sustainability. The rhizosphere comprises three distinct zones viz., endorhizosphere, rhizoplane and ectorhizosphere. The rhizosphere should be viewed as a gradient of chemical, biological and physical qualities along the root rather than as a zone with a defined size or shape. Plant metabolism has a major effect on the rhizosphere through the release of carbon dioxide (CO$_2$) and the secretion of photosynthate as a variety of root exudates (mostly from the ectorhizosphere and rhizoplane). By providing microorganisms with energy and functioning as chemical attractants and repellents, root exudates, which include phytohormones, promote interactions between the rhizosphere and other environments. Agronomic functions like crop production, nutrient trapping, carbon uptake and storage and the cycling of water and carbon are all dependent on the rhizosphere (Adl, 2016). There are several direct and indirect ways that the rhizosphere ecology and consequently, ecosystem function will be impacted by global climate change, which includes increased temperatures and altered weather patterns brought on by growing atmospheric CO$_2$ levels.

Abiotic stressors like drought, high temperatures and salinity are the main reasons for crop yield decline, loss of native vegetation and consequently, a decrease in the plant’s ability to absorb CO$_2$. Photosynthesis and root development are significantly inhibited by drought stress (Verslues, 2017). Excessive concentrations of Na$^+$ and Cl$^-$ in salinity stress result in ion toxicity, which has a negative impact on plant development and growth (Negrao et al., 2017). Stressors like salinity and drought both raise ethylene levels, which limit root growth and have an impact on several physiological pathways in plants. Other external stressors have a detrimental effect on plant growth and development in a variety of ways, such as upsetting hormone balance and making plants more susceptible to illness.

Extensive physiological adaptations are necessary for plant survival under abiotic stress conditions. Accordingly, plant hormones are essential for the development and expansion of roots as well as the control of their morphological reactions to abiotic stress. Abiotic stressors can disrupt the complex network formed by hormone sensing and crosstalk, changing the rhizosphere’s root development. Almost every aspect of plant growth and development is primarily regulated by the phytohormone auxin. The rise in root hair length, the bimodal influence of auxin concentration on primary root length, the dose-dependent increase in lateral root primordia number and the response to gravity are the most significant auxin-associated phenotypes in roots (Overvoorde et al., 2010).

Gibberellic acids (Gas) and cytokinin’s, two other classes of plant hormones, function as positive stimulators of root elongation and negative regulators of root development respectively. Exogenous cytokinin treatment has been demonstrated to prevent root extension but endogenous cytokinin level reduction promotes primary root elongation. It is generally known that abscisic acid (ABA) has a role in reactions to abiotic stressors, particularly drought. The ABA production in the root tips increases in response to a decrease in soil water in the rhizosphere region. This enhanced
biosynthesis is subsequently transferred to the leaves, where it induces stomatal closure. According to studies (Smith and De Smet, 2012) ABA is known to impede primary root elongation during drought stress.

Plant growth and development are greatly influenced by ethylene, a gaseous hormone that is present in plants. As per Negi et al. (2008), ethylene strongly inhibits the extension of roots and shoots, strigolactones and their derivatives have recently been identified. Specifically, according to Sun et al. (2016), strigolactones and their derivatives inhibit the growth of lateral roots while encouraging the elongation of primary and adventitious roots. It is important to remember that hormonal crosstalk plays a crucial role in the development and growth of plants. For instance, ethylene stimulates the expression of genes involved in auxin biosynthesis, AUX1 (auxin transporter protein 1), PIN2 (PIN FORMED 2 auxin transporter) and other auxin transporters, leading to an increase in basipetal auxin transport. This regulates auxin transport within the root tip, effectively controlling root formation. Concerning the advantageous interactions between plants and microbes, plant phytohormones are also very much important. Thus, in all endeavors pertaining to rhizosphere engineering plant phytohormones ought to be regarded as important components.

According to Farrar et al. (2014) plants can boost their resistance to abiotic challenges by interacting with naturally occurring microbes, however they can also adapt to these stresses through phenotypic plasticity. The microbiome of plants is sometimes referred to as the second genome of the plant because of the close relationship that plants have with microorganisms. Plants may be viewed as meta-organisms or holobionts between the plant and its interacting microbiota (Vandenkoornhuyse et al., 2015). Numerous isolated bacterial strains have been identified as plant growth-promoting bacteria (PGPB), as will be further explained below. PGPBs can promote plant growth through a variety of direct and indirect processes. These mechanisms include the release of plant growth regulators, organic acids, volatile organic compounds (VOCs), biological nitrogen fixation, induction of systemic resistance and protection by enzymes such as chitinase, glucanase and 1-aminocyclopropane-1-carboxylate (ACC)-deaminase.

Many competing and interacting processes that rely on the type and water content of the soil, the makeup of microbial communities and the physiology of the plant itself create the physical and chemical environment of the rhizosphere. All three rhizosphere components- plant, soil and microbes can be manipulated for increased plant productivity. Plants can be engineered to carry novel and beneficial traits of interest, microbiomes can be selected for beneficial traits like promoting plant growth and root characteristics and the soil can be amended or managed to improve its overall quality by changing its physical and chemical properties. Nutrient bioavailability can be enhanced by the use of artificial and natural plant-microbe interactions.

To further improve the interactions between microbes and plant roots, genetic engineering can be utilized to target the important chemical molecules involved in these interactions for abiotic stress tolerance. The primary focus of this review is on the role of plants and microbes (PGPRs) in rhizosphere engineering.

**Rhizosphere engineering**

The rhizosphere refers to the narrow region of soil immediately surrounding plant roots, which serves as a hub for diverse microorganisms. This zone of soil in the
rhizosphere tends to be conducive to the growth of microbial populations, falling within the mesotrophic range. The rhizosphere can be intentionally manipulated or harnessed to fulfill various functions, including nutrient cycling, protection against phytopathogens, and shielding plants from abiotic stress conditions. The interaction of plants and microbes has an effect on overall performance and productivity (Masood et al., 2020; Balamurugan et al., 2023). Rhizosphere engineering holds the potential to reduce our dependency on agrochemicals by substituting their roles with beneficial microbes, environmentally friendly biostimulants, or genetically modified plants. Various factors exert an influence on the activity within the rhizosphere in relation to plant health and growth.

Several factors play a role in influencing rhizosphere activity in plants:
1. Carbon dioxide (CO₂) concentration and exudation of photosynthates and root exudates.
2. Physical and chemical characteristics of the soil, along with microbiome composition.
3. Environmental stressors such as drought, high temperatures and salinity.

Hence, it is essential to recognize plant phytohormones as a fundamental element in all initiatives related to rhizosphere engineering (Figs. 1 and 2). These phytohormones operate through various mechanisms, including their wide-ranging role in countering soil-borne pathogens, sequestering nutrients, triggering the synthesis of plant hormones and nitrogen fixation, exemplified by organisms like bradyrhizobium and rhizobium.

Components of rhizosphere engineering

The concept of rhizosphere engineering encompasses three fundamental components: plants, microbes, and soil (Fig. 2). Each of these elements can be intentionally modified to enhance plant productivity. Soil amendments, including substances like biochar and silicon, zeolites, crop residues, coal fly ash, animal manure, and sewage sludge (Dessaux et al., 2016), have been effectively employed to influence rhizosphere dynamics, ultimately promoting plant growth. Given that the activity and functionality of the rhizosphere are intricately linked to plant characteristics such as root architecture and root exudates, genetic engineering of plants can be harnessed to intentionally modify these traits. Numerous plant species have undergone genetic modifications using breeding and gene editing approaches to improve nutrient uptake, including phosphorus, iron, and zinc. Furthermore, genetic engineering has been applied to enhance diseases resistance and to remove heavy metals.

Role of plant growth-promoting microbes in rhizosphere engineering

The modern agriculture highly depends on fertilizers and pesticides. With the continuous application of chemicals causing low soil fertility and pest and disease resistant of crops are breaking down (Dhanushkodi and Nageswari, 2022). Plant growth-promoting microbes play a crucial role in enhancing plant growth and addressing various challenges in modern agriculture (Table 1). Within the rhizosphere microbiome, a significant portion comprises bacteria known as plant growth-promoting rhizobacteria (PGPR), with only a limited number found to be harmful to plants (Kumar
and Dubey, 2020). These beneficial microbes also contribute to the mineralization of organic pollutants and are employed in the bioremediation of contaminated soils (Bibi et al., 2018). Actinomycetes, another group of microorganisms, enhance plant productivity (Muleta and Assefa, 2018), while various bacterial communities are present in root nodules, leaves, and stems (Kumar and Dubey, 2020).

![Figure 1. Rhizosphere engineering with PGPR (Hakim et al., 2021)](image1)

![Figure 2. Components of rhizosphere engineering and their complex interactions (Hakim et al., 2021)](image2)
**Table 1.** List of the Bacteria used as inoculums and co inoculums in agriculture

<table>
<thead>
<tr>
<th>S. No.</th>
<th>Name of the Bacteria used as inoculums and co inoculums</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td><em>Rhizobium, Sinorhizobium, Bradyrhizobium, Allorhizobium, Ochrobactrum, Mesorhizobium and Pseudomonas</em></td>
<td>Hakim et al., 2020; Ahmad et al., 2012</td>
</tr>
<tr>
<td>2</td>
<td><em>Arthrobacter, Curtobacterium, Micromonospora, Microbacterium, Mycobacterium, Acinetobacter, Agrobacterium, Blastobacter, Bosea, Devosia, Herbaspirillum, Pantoena, Pseudomonas, Ralstonia, Stenotrophomonas, Bacillus, Brevi bacillus, Paenibacillus, Chryseobacterium, and Sphingobacterium</em></td>
<td>Hakim et al., 2020</td>
</tr>
<tr>
<td>3</td>
<td><em>Arthrobacter, Bacillus, Azotobacter, Micrococcus, Pseudomonas, and Serratia</em></td>
<td>Adesemoye and Egamberdieva, 2013</td>
</tr>
<tr>
<td>4</td>
<td><em>Acetobacter, Azospirillum, Micromonospora, Paenibacillus, Enterobacter, Herbaspirillum, Serratia, Rhodococcus, Bradyrhizobium strain and Streptomyces</em></td>
<td>Htwe et al., 2018</td>
</tr>
<tr>
<td>5</td>
<td><em>Bacillus megaterium, Paenibacilluspolymyxa and Rhizobium</em></td>
<td>Korir et al., 2017</td>
</tr>
</tbody>
</table>

**Rhizosphere engineering through plant biotechnology**

The realm of rhizosphere engineering has seen significant progress in plant biotechnology, particularly in the identification of genes that govern root exudates. This advancement offers the potential to alter the levels of the plant genes, thereby reshaping the rhizosphere to enhance its beneficial characteristics. As an illustration of this concept, rice and tomato were genetically modified with the Arabidopsis vacuolar H⁺-pyrophosphatase gene, AVP1. These transformed plants showed approximately 50% higher citrate and malate efflux compared to their wild-type counterparts when exposed to AlPO₄. This effect was taken as a strategy to bolster resistance to Al³⁺ stress and improve the plant’s capacity to access insoluble phosphorus. However, it is crucial to recognize that engineering plants to influence the rhizosphere can be a complex undertaking. These complexities underscore the need for comprehensive research and careful consideration when applying plant biotechnology to rhizosphere engineering. While constitutive overexpression of single genes encoding enzymes linked to the accumulation of osmolytes and proteins that serve as reactive oxygen species (ROS) scavengers and ion transporters has been the most widely used method for enhancing abiotic stress tolerance in plants, transcriptome engineering is a promising technique for producing abiotic stress tolerant crops (Reguera et al., 2012).

One important method to examine the host genome for particular gene pools linked to different phenotypic features is to apply the quantitative trait locus (QTL) mapping methodology. When a suitable gene pool has been identified in the plant genome, sophisticated genome editing tools can be applied to modify the traits for the purpose of attracting the desired rhizosphere microbiome. These tools include zinc finger nucleases (ZFNs), clustered repeatedly interspaced short palindrome repeats (CRISPR)/CRISPR – associated protein 9 (Cas 9) and site-specific transcription activator – like effector nucleases (TALENs) (Kaul et al., 2021; Kumar and Dubey, 2020).

By focusing on important genes at the transcriptional and translational stages, these instruments can influence biosynthetic and metabolic processes. The CRISPR/Cas9 system is the most cutting – edge technique available for deleting or
introducing important genes into numerous plants. Using this method, a study created a tomato plant that was resistant to the pathogen *Pseudomonas syringae* pv. Tomato (Pto) DC3000, which causes bacterial speck disease (Ortigosa et al., 2019). Moreover, by deleting the TaMLO gene which is linked to the colonization of fungi from the protoplasts of a wheat cultivar, Shan et al. (2014) were able to successfully create a cultivar resistant to powdery mildew disease. As a tool for genome editing, the CRISPR/Cas9 system has yielded many more successes and there is yet much more to come.

Recently, plant microbiome engineering has come under the spotlight with a number of accessible approaches (*Fig. 3*). Microorganisms found in such a biome tend to alter plant physiological function and enable plants to resist harmful invasions (Dubey et al., 2019; Santoyo et al., 2021). This type of microbe clusters on the surface and within the tissues of the host plant as part of its microbiome. The development of novel stress tolerance, disease resistance and nutrient acquisition strategies for host plants has been proposed through soil amendment, artificial microbial consortia and host-dependent microbiome engineering (*Fig. 3*).

- Host-mediated microbiome: Indirectly selection of microbiome through utilization of host phenotype.
- Artificial seed microbiome: The integration/inoculation of artificially selected microbiota into seeds. Accordingly, the structure and function of the plant microbiome may be affected as the microbiome changes during growth and germination.
- Rhizosphere microbiome: Engineering bacterial competitiveness.
- Synthetic microbiome: Inoculation of host plants with genetically modified microorganisms.
- In situ microbiome: Native microbiological communities are manipulated within their natural environments.
- Plant microbiome: Enhancement and refinement of advantageous plant-fungal dynamics.

*Figure 3. Plant microbiome engineering via biotechnological and conventional approaches (Muhammad Siddique Afridi et al., 2022)*
Genomic approaches in root associated interactions

Recently, the initiation of omic tools related to the techniques like gene-editing, and sequencing technology has allowed us to focus the interlink of plant-microbes interactions, resulting on enhancement of plant healthy subsistence and tolerance to biotic and abiotic challenges. Genomics approach helps in interpretation on interactions of microbes- plants and developing pathogen stress tolerance in plants (Frantzeskakis et al., 2020). High genetic variability in the soil microbiome can be confirmed by multiple sequencing methodologies, such as prokaryotic16S, fungal ITS (internal transcribed spacer regions), and/or metagenomic analysis. The microbiome composition can be altered by environmental factors such as soil physio-chemical properties. In addition, plant biochemistry and the immune system also play key roles in microbiome existence in that microenvironment that can be probed through metagenomics, which offer a promising strategy to diagnose these phytopathogens (Chiu and Miller, 2019).

Recently, nanopore sequencing using Oxford Nanopore Technologies (ONT) is the most encouraging technology for the microbial identification metagenome sequencing (Jain et al., 2016) having an advantage of fast and direct sequencing method requiring no amplification step. Therefore, it can be combined with Illumina technologies to enhance the sequence assembly quality (Sevim et al., 2019). Low sequencing cost and high quality suggest that direct sequencing (Ciuffreda et al., 2021) are likely to be the future tool and becoming feasible because of the expanding information in metagenomics. These strategies would be helpful for initial molecular assessment of the soil and soil microbiome could help in the improvement of agricultural treatments. Conversely, the complimentary response of the host toward beneficial microbes should also be a part of the rhizosphere engineering program because the host is also involved in bringing the interaction. The drawback of genomic analysis is that it does not provide knowledge about the functional states of biological objects; therefore, a metagenomics approach can be used in combination with a transcriptomic approach to evaluate key traits in plant-microbiome interactions. Next Generation Sequencing (NGS)-based transcriptomics is another approach used for through molecular mechanisms involved in plant–microbiome interactions. It is usually applied in plant protection and plant stress management studies where they characterize the signaling events that happens in rhizosphere.

Over the past few decades, industrialization and urbanization have caused an increase in carbon dioxide and temperature, which affect the climate globally. These changes cause erratic events worldwide, such as a decrease in moisture level, an increase in temperature, excessive greenhouse gas emissions, and an increase in snowfall and rainfall. Climate change, range shift and urbanization are key factors that affect plant microbial interactions in the rhizosphere. Soil microbial community determines the soil, and plant health and prerequisite for external constraints. Soil microbial ecosystem functions and diversity are significantly influenced by anthropogenic activities These activities produce a diverse array of hazardous substances including pesticides, heavy metals (Ma et al., 2022) and organic pollutants and put tremendous pressure on soil microbiomes. Heavy metals notoriously imbalance the microbial population, diversity and seriously decline their activities (Fajardo et al., 2019; Li et al., 2020).

Metabolic engineering

Despite the efforts devoted to increase and diversify bioactive compounds in plants, it is still a challenge as to how to increase their content in vivo and, as mentioned
before, how to obtain reproducibility of bioactive under field production conditions. These efforts rely on transgenic and non-transgenic approaches which involve complex regulation mechanisms that are required for increasing the levels of functional metabolites in plants. Bacterial elicitors may be used to determine the key genes limiting a metabolic pathway once the limiting step is identified. Transgenic approaches may allow us to overcome the low levels of target compounds produced. Finally, and this is a very attractive and encouraging challenge, upon elicitation, new molecules may appear after the activation of a given metabolic pathway.

Rhizosphere engineering using synthetic microbial communities

The concept of rhizosphere engineering has evolved to include the structure microbial communities designed to promote crop growth, enhance disease resistance, and regulate stress tolerance (Fig. 4).

This approach offers a distinctive opportunity in the realm of bioengineering. Although numerous bacterial strains have been recognized for their various beneficial effects, creating a sustainable synthetic microbial community presents a formidable task. The complexity of these potential ecological interactions increases linearly with the addition of extra strains. The primary challenges revolve around positive effects and cooperation within the synthetic microbial community due to minimizing parasitism and competition. Reducing race is mainly daunting, as even in two-strain co-cultures, competition tends to dominate quickly (Foster and Bell, 2012). Many microbial genera are well-suited for rhizosphere colonization, possess publicly available genome sequences, and are amenable to genetic engineering efforts. While Streptomyces spp. are noteworthy examples of plant growth-promoting rhizobacteria (PGPRs) with
tractable genetic systems and numerous complete genome sequences, they come with certain limitations, such as large genomes and numerous mobile elements that hinder engineering and growth in cooperative synthetic microbial communities. As a foundational element of a synthetic community, Bacillus spp. are chosen for their relative ease of genetic engineering, abundant complete genome sequences (Sharma and Satyanarayana, 2013), and the presence of isolates with plant growth-promoting properties.

**Nutrient mobilization in the rhizosphere**

Food and Agricultural Organization (FAO) form a concept on incorporation or use of locally available and all possible nutrient resources in crop production for better resource use and to improve agriculture productivity (*Table 2*). In the present era, enhancing the efficiency of fertilizer use and ensuring the long-term viability of agriculture are paramount concerns (Karunakaran et al., 2010). Plant growth-promoting bacteria (PGPR) and the engineering of the rhizosphere play pivotal roles in this endeavor.

*Table 2. Nutrient mobilization in the rhizosphere*

<table>
<thead>
<tr>
<th>Nutrients</th>
<th>Bacteria involved</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Phosphorus</td>
<td>Gordonia, Klebsiella, Arthrobacter, Bacillus, Pseudomonas, Serratia, Brevundimonas, Delftia, Enterobacter, Phyllobacterium and Xanthomonas</td>
<td>Alori et al., 2017</td>
</tr>
<tr>
<td>Zinc</td>
<td>Acinetobacter, P. striata, Bacillus thuringiensis, Burkholderiaconcepsia, Serratia liquefaciens, Pseudomonas aeruginosa, Gluconactetobacter diazotrophicus and S. marcescens</td>
<td>Kumar et al., 2019</td>
</tr>
<tr>
<td>Iron</td>
<td>Agrobacterium tumefaciens, Azospirillum, Azotobacter, Bacillus, Enterobacter, Mycobacterium, Neisseria gonorhooae, Paracoccus denitrificans, P. fluorescens, Rhizobium meliloti, Serratia, and Streptomyces</td>
<td>Zhang et al., 2019</td>
</tr>
<tr>
<td>Nitrogen</td>
<td>Symbiotic N$_2$ fixing bacteria: <em>Rhizobium</em>, <em>Bradyrhizobium</em>, <em>Ensifer</em>, <em>Azorhizobium</em>, and <em>Mesorhizobium</em></td>
<td>Masood et al., 2020</td>
</tr>
<tr>
<td></td>
<td>Non-symbiotic diazotrophic bacteria: <em>Arthrobacter</em>, <em>Azotococcus</em>, <em>Azospirillum</em>, <em>Azotobacter</em>, <em>Enterobacter</em>, <em>Mitsuaria</em>, <em>Pseudomonas</em></td>
<td></td>
</tr>
</tbody>
</table>

Plant growth inducing by directly releasing microbial exudates (such as metabolites and tiny peptides/lipids) in the rhizosphere, a type of PGPBs known as rhizobacteria (PGPR) live the surface or close proximity to the roots and aid in the promotion of plant growth and development. Their modes of action include direct fixation of nitrogen (*Bradyrhizobium* and *Rhizobium*), immobilization of nutrients (phosphorus), and release of plant hormones and broad spectrum antagonistic biocontrol of soil-borne pathogens (*Table 3*.). Hundreds of rhizospheric isolates have produced axenic cultures with PGPR properties (Bhattacharyya and Jha, 2012).

**Mitigating abiotic stress in the rhizosphere**

The survival of plants under challenging abiotic stress conditions necessitates significant physiological adaptations (*Fig. 5*). Plant hormones, including auxin (Overvoorde et al., 2010), cytokinins, gibberellic acids, abscisic acid (Smith and Smet, 2012), ethylene and strigolactones (Sun et al., 2016), assume critical roles in root development, growth, and responses to abiotic stressors. Within this context, the
perception and intricate crosstalk among these hormones form a complex network in which abiotic stresses can disrupt, leading to alterations in root growth within the rhizosphere.

**Table 3. Role of rhizosphere engineering with PGPR on plant growth and stress tolerance**

<table>
<thead>
<tr>
<th>S. No.</th>
<th>Rhizosphere/plant host</th>
<th>Microbes used</th>
<th>Effect on plant/soil</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Wheat</td>
<td><em>Enterobacter sp., A. chlorophenolicus, S. marcescens, B. megaterium</em></td>
<td>Phosphorus solubilization, HCN, N-fixation, gibberellin, siderophores</td>
<td>Kumar et al., 2015</td>
</tr>
<tr>
<td>2</td>
<td>Soybean</td>
<td><em>Bacillus cereus</em> Sideophore</td>
<td>IAA, phosphorus solubilization, EPS</td>
<td>Arif et al., 2017</td>
</tr>
<tr>
<td>3</td>
<td>Arabidopsis thaliana</td>
<td><em>Bacillus amyloliquefaciens</em></td>
<td>Production of phytohormone, lipopeptide</td>
<td>Asari et al., 2017</td>
</tr>
<tr>
<td>4</td>
<td>Tomato</td>
<td><em>Bacillus pumilus, Bacillus amyloliquefaciens</em></td>
<td>HCN, siderophore, N-fixation, IAA, P-solubilization</td>
<td>Xiaohui et al., 2017</td>
</tr>
<tr>
<td>5</td>
<td>Potato</td>
<td><em>Brevundimonas spp. Azospirillum sp.</em></td>
<td>Phosphorus solubilization, N-fixation, IAA production</td>
<td>Naqqash et al., 2020, 2016</td>
</tr>
<tr>
<td>6</td>
<td>Potato, Rice, wheat, maize, soybean</td>
<td><em>Serratia spp.</em></td>
<td>AHLs, IAA production, phytase activity</td>
<td>Hanif et al., 2020</td>
</tr>
<tr>
<td>7</td>
<td>Pea</td>
<td><em>Azospirillum, Agrobacterium tumefaciens</em></td>
<td>N-fixation, phosphorus solubilization</td>
<td>Ejaz et al., 2020</td>
</tr>
<tr>
<td>8</td>
<td>Rice</td>
<td><em>Achromobacter xylosoxidans, Azospirillum brasilense, Bacillus subtilis, Bacillus megaterium, Pseudomonas stutzeri, Rhodococcus rhodochrous</em></td>
<td>Phosphorus solubilization, ACC deaminase activity, siderophores production</td>
<td>Rasul et al., 2019</td>
</tr>
<tr>
<td>9</td>
<td>Maize</td>
<td><em>Mesorhizobium ciceri, Ochrobactrum ciceri, Serratia marcescens</em></td>
<td>IAA production, phosphorus solubilization and zinc solubilization</td>
<td>Zahid, 2015</td>
</tr>
<tr>
<td>10</td>
<td>Chickpea</td>
<td><em>Bacillus amyloliquefaciens,</em></td>
<td>Phosphorus solubilization, IAA production, nitrogen fixation</td>
<td>Zaheer et al., 2016</td>
</tr>
<tr>
<td>11</td>
<td>Cotton</td>
<td><em>Bacillus amyloliquefaciens,</em></td>
<td>Production of phytohormones, N-fixation, phosphorus solubilization, and antibiotic activity</td>
<td>Fahimi et al., 2014</td>
</tr>
<tr>
<td>12</td>
<td>Mung bean</td>
<td><em>Rhizobium, Bradyrhizobium, Bacillus cereus, B. drentensis, B. pumilus, B. subtilis, Enterobacter cloacae, Pseudomonas putida, Ochrobactrum</em></td>
<td>N-fixation, phosphorus solubilization, IAA production, siderophore production, ACC-deaminase activity</td>
<td>Mahmood et al., 2016</td>
</tr>
<tr>
<td>13</td>
<td>Cabbage</td>
<td><em>Bacillus subtilis</em></td>
<td>Gibberellins production</td>
<td>Kang et al., 2019</td>
</tr>
<tr>
<td>14</td>
<td>Groundnut</td>
<td>Vasicular Arbicular Mychorhyza</td>
<td>Phosphorous mobilization</td>
<td>Brindavathy and Vaidyanathan, 2017</td>
</tr>
<tr>
<td>15</td>
<td>Moth Bean</td>
<td><em>Rhizobium skierniewicense</em></td>
<td>N-fixation, siderophore production, drought tolerant indices</td>
<td>Brindavathy et al., 2022</td>
</tr>
<tr>
<td>16</td>
<td>Sugarcane</td>
<td><em>Bacillus megaterium</em></td>
<td>Silicon solubilizing under drought</td>
<td>Anitha et al., 2023</td>
</tr>
</tbody>
</table>
Rhizosphere effects in drought management

Drought stands out as the single most formidable threat to plant and crop productivity, surpassing all other environmental factors in its capacity to hinder plant growth and development (Anjum et al., 2011; Sritharan et al., 2015). The most significant hazard to agricultural and plant productivity is drought; it hinders plant growth and development more than any other environmental element. Factors pertaining to climate, edaphics and agronomy influence drought stress and future projections indicate that the effects of drought will worsen due to climate change and the reduction of freshwater resources worldwide. Therefore, in addition to the pressing need for developing drought-tolerant crops to ensure food security, there arises an equally compelling imperative to enhance drought tolerance and WUE in bioenergy crop plantations. This is particularly crucial for ensuring sustainable biomass production in arid and semi-arid regions. In this endeavor, the rhizosphere and its associated microbiota play pivotal roles in regulating a plant’s and plant ecosystems’ ability to adapt and withstand the challenges posed by drought (Table 4).

The ability of plants ecosystems to withstand is largely regulated by the rhizosphere and related bacteria. Plant PGPRs colonize the rhizosphere/endo-rhizosphere and confer drought tolerance through the following mechanisms: (i) Production of exopolysaccharides (EPS), 1-aminocyclopropane-1-carboxylate (ACC) deaminase, volatile organic compounds (VOCs) and phytohormones such as gibberellic acid, cytokinins, abscisic acid (ABA) and indole-3-acetic acid (IAA) (ii) inducing accumulation of osmolytes and antioxidants and (iii) Regulation of stress-responsive genes and change in root morphology (Vurukonda et al., 2016). By promoting root growth and the development of lateral roots, IAA—promoting root growth and the development of lateral roots, IAA – producing Azospirillum spp. Increased wheat tolerance to drought stress. Similar to this, PGPR Bacillus thuringiensis enhanced the
nutrition, physiology and metabolic activities of a lavender species (*Lavandula dentate*) by producing IAA, which promoted the plant’s development in drought-stricken conditions (Armada et al., 2014). Similarly, Rolli et al. (2015) have shown how isolates of GFP-labelled *Acinetobacter* spp. and *Pseudomonas* spp. Improve drought tolerance in Arabidopsis and grapevine via a mechanism caused by water stress.

**Table 4. Rhizosphere intervention against drought**

<table>
<thead>
<tr>
<th>S. No.</th>
<th>Crop</th>
<th>PGPR</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Wheat</td>
<td><em>Azospirillum sp</em></td>
<td>Arzanesh et al., 2011</td>
</tr>
<tr>
<td>2</td>
<td><em>Lavandula dentate</em></td>
<td><em>Bacillus thuringiensis</em></td>
<td>Armada et al., 2015</td>
</tr>
<tr>
<td>3</td>
<td>Arabidopsis and grapevine</td>
<td>GFP-labelled <em>Acinetobacter</em> spp. and <em>Pseudomonas</em> spp. isolates</td>
<td>Rolli et al., 2015</td>
</tr>
<tr>
<td>4</td>
<td><em>Platycladus orientalis</em></td>
<td><em>Bacillus subtilis</em></td>
<td>Liu et al., 2013</td>
</tr>
<tr>
<td>5</td>
<td><em>Brassica napus</em></td>
<td><em>Phyllobacterium brassicaeearum</em></td>
<td>Bresson et al., 2013</td>
</tr>
<tr>
<td>6</td>
<td>Soybean</td>
<td><em>Pseudomonas putida</em> strain H-2-3</td>
<td>Kang et al., 2014b</td>
</tr>
<tr>
<td>7</td>
<td>Wheat</td>
<td><em>Bacillus thuringiensis</em> strain AZP2 and <em>Paenibacillus polymyxa</em> strain B</td>
<td>Timmusk et al., 2014</td>
</tr>
<tr>
<td>8</td>
<td>Soybean (Glycine max)</td>
<td><em>Pseudomonas fluorescens</em>, <em>Azospirillum sp.</em>, <em>Bacillus pumilus</em>, <em>Rhizobium japonicum</em>, <em>Azotobacter chroococcum</em>, <em>Azospirillum brasiliense</em></td>
<td>Zahedi and Abbasi, 2015</td>
</tr>
</tbody>
</table>

In a different study, it was demonstrated that *Phyllobacterium brassicaeearum* strain STM196, which was isolated from the oilseed rape (*Brassica napus*) rhizosphere, could improve osmotic stress tolerance in inoculated Arabidopsis plants by boosting ABA levels and reducing leaf transpiration. This helped the plants cope with drought stress (Bresson et al., 2013). Additionally, it was discovered that under drought stress, soybean plant infected with the gibberellin – producing rhizobacterium *Pseudomonas putida* strain H-2-3 displayed increased shoot length and fresh weight. In response to stress, these soybean plant also accumulated larger levels of abscisic acid, salicylic acid and chlorophylls than control plants (Kang et al., 2014b). Timmusk et al. (2014) used a promising method to prepare wheat plants by isolating soil microbial communities from severe settings. *Bacillus thuringiensis* strain AZP2 and *Paenibacillus polymyxa* strain B were able to give wheat seedlings enhanced resistance out of a dozen or more isolates.

**Salinity and its impact on plant productivity**

Salinity stands as a significant environmental stressor that exerts a severe impact on plant productivity on a global scale. Elevated salt levels in the soil lead to ion toxicity and disrupt ion balances within plants, ultimately resulting in metabolic disruptions and the imposition of hyperosmotic stress-induced water deficits (Anitha et al., 2015). In response to salinity stress, plants employ various mechanisms to adapt and cope, including the synthesis of osmolytes and polyamines, activation of defense mechanisms, reduction of reactive oxygen species (ROS) accumulation, and adjustments in ion transport and compartmentalization.

In order to combat the effects of salinity stress, plants produce polyamines and osmolytes, activate defense systems and decrease ROS buildup, ion transport and
compartmentalization (Table 5). Inoculated wheat seedlings with EPS-producing PGPRs (such as *Bacillus* spp., *Enterobacter* spp., and *Paenibacillus* spp.) showed markedly reduced Na\(^+\) absorption and enhanced biomass production in high-saline conditions in a study by Upadhyay et al. (2011). Additionally, it was demonstrated that inoculated tomato plants with specific PGPRs could continue to develop in high-salinity and water-limited environments by mitigating the detrimental effects of stress induced ethylene release on root growth via the action of the bacterium ACC-deminase.

In a recent work, Bharti et al. (2016) showed how to give wheat salinity resistance by using a PGPR Dietzia natronolimnaea strain STR1, which produces carotenoids. According to Bharti et al. (2016), inoculated plants were able to tolerate salinity stress because they expressed more proline and other antioxidants. In addition, the PGPR injection caused these plant’s ABA signaling, SOS pathways and iron transport to become active. Similarly, salt tolerance was conferred in peanut seedlings by five bacterial isolates from the genera *Klebsiella*, *Pseudomonas*, *Agrobacterium* and *Ochrobactrum*. When exposed to salt stress, peanut seedlings grew more rapidly than non-inoculated seedlings, maintained ion homestasis and had decreased ROS accumulation (Sharma et al., 2016).

<table>
<thead>
<tr>
<th>S. No.</th>
<th>Crop</th>
<th>PGPR</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Wheat</td>
<td><em>Bacillus</em> spp., <em>Enterobacter</em> spp., <em>Paenibacillus</em> spp.</td>
<td>Upadhyay et al., 2011</td>
</tr>
<tr>
<td>2</td>
<td>Wheat and Peanut</td>
<td><em>Dietzia natronolimnaea</em> strain STR1, <em>Klebsiella</em>, <em>Pseudomonas</em>, <em>Agrobacterium</em>, and <em>Ochrobactrum</em></td>
<td>Bharti et al., 2016</td>
</tr>
<tr>
<td>3</td>
<td>Mung beans</td>
<td><em>Enterobacter cloacae</em> and <em>Bacillus drentensis</em></td>
<td>Mahmood et al., 2016</td>
</tr>
<tr>
<td>4</td>
<td>Peanuts</td>
<td><em>Brachybacterium saurash trense</em> strain JG-06, <em>Brevibacterium casei</em> strain JG-08, and <em>Haererohalobacter</em> spp. strain JG-11</td>
<td>Shukla et al., 2012</td>
</tr>
<tr>
<td>5</td>
<td>Pepper</td>
<td><em>Bacillus</em> spp., <em>Paenibacillus</em> spp., <em>Bacillus subtilis</em></td>
<td>Lim and Kim, 2013</td>
</tr>
<tr>
<td>6</td>
<td>Sugarcane</td>
<td><em>Azotobacter chroococcum</em>, <em>Bacillus subtilis</em>, <em>Aeromonas salmonicida</em>, <em>Burkholderia cepacia</em>, <em>Ochrobactrum anthropi</em>, <em>Pseudomonas</em> sp., <em>Shewanella putrefaciens</em>, <em>Sphingomonas paucimobilis</em>, <em>Stenotrophomonas maltophilia</em>, <em>Brevibacterium</em>, <em>Burkholderia</em>, <em>Delftia</em>, <em>Leucobacter</em>, <em>Pseudomonas</em>, <em>Sinorhizobium</em> and <em>Variovorax</em></td>
<td>Solanki et al., 2017</td>
</tr>
</tbody>
</table>

### Table 5. Mitigating salinity through rhizosphere interventions

**Increased atmospheric CO₂ concentrations**

Plants absorb carbon dioxide (CO₂) from the atmosphere through photosynthesis, storing it as organic carbon in various plant compartments or transferring it to microbial biomass and the soil, particularly via root allocation. The potential of plant growth-promoting rhizobacteria (PGPRs) to enhance terrestrial carbon storage has been explored, with the aim of augmenting plant productivity and mitigating carbon losses
due to microbial respiration in the context of rising atmospheric CO₂ levels, (Nie et al., 2015). Consequently, it is conceivable that elevated atmospheric CO₂ levels projected in future climate scenarios could lead to an increased prevalence of PGPRs in the rhizosphere.

Rhizospheric microorganisms may be stimulated by enhanced C3 photosynthesis brought on by rising atmospheric CO₂ levels because of an increase in photosynthate transfer to the soil. Changes in plant diversity and composition brought on by the climate will have a longer-term impact on the soil and soil microorganisms, which will change the amount and quality of soil organic matter. It is obvious that these influences of soil characteristics and soil biota, both caused by climate change and plant-mediated, will have significant consequences on the cycling of carbon, the intake of methane and nitrous oxide and the climate in terrestrial ecosystems.

Thus, increased atmospheric CO₂ levels under future climatic scenarios may contribute to PGPR domination. It is mainly unknown how these relationships between plants and microbes are formed, how a host plants’ microbiome affects its productivity and how specific microorganisms reduce plant stress. To maximize the benefits of PGPB in enhancing plant ecosystem performance, then, not only mechanisms responsible for promoting plant growth be extensively researched, but also a comprehensive understanding of all the phase involved in plant colonization by bacteria be attained.

**Waterlogging stress on microbial diversity**

Plants require adequate water to grow normally, but waterlogging stress can quickly result from saturation or even super-saturated of the soils’ water-holding capacity. Inhibiting root respiration and allowing harmful compounds to build up during waterlogging stress negatively impact both vegetative and reproductive growth, ultimately resulting in yield loss or even total harvest failure (Tian et al., 2019; Ding et al., 2020; Zhou et al., 2020).

According to Yan et al. (2018), waterlogging causes leaf stomata to close, while chlorophyll deterioration, leaf senescence and yellowing lessen the leaves’ capacity to absorb light and ultimately cause a decrease in the photosynthetic rate. Since the oxygen diffusion rate in water is just 1/10,000 of that in air, waterlogging blocks the exchange of gases between the soil and atmosphere by removing air from soil pores. According to Van Veen et al. (2014), this leads to a significant restriction of oxygen availability in wet soil, which in turn causes a suppression of root respiration, a decrease in root activity and an energy deficit.

The major variables limiting crop productivity are flooding (which further promotes submergence), hypoxia and waterlogging stress. A hypoxic environment is produced in the rhizosphere by flooding, which forces submergence and eventually elevates the ground water table. According to Fukao et al. (2019), the hypoxic condition in the rhizosphere limits the uptake of oxygen by creating an anaerobic environment, which further results in plant death. As a result, the stressors of flooding, submergence and waterlogging are related to each other and have a nearly similar effect on the plant.

One of the most detrimental effects is the sharp reduction in soil oxygen levels, which has adverse consequences for microbial diversity and community activity (Yang et al., 2016). This stress condition can also lead to the loss of nitrogen. Consequently, collaborative efforts are essential to mitigate the detrimental effects of waterlogging stress on crop production (Ngumbi and Kloepper, 2016). Beneficial bacteria, such as
those containing 1-aminocyclopropane-1-carboxylic acid deaminase, like Bacillus, have the potential to alleviate waterlogging-induced stress by reducing ethylene levels, thus safeguarding plants from the adverse effects of waterlogging (Nascimento et al., 2014). Additionally, Bacillus thuringiensis can synthesize indole-3-acetic acid in the rhizosphere, contributing to improved plant resilience (Armada et al., 2015). Furthermore, the presence of microorganisms like Flavisolibacter and Massilia can aid in phosphorus mobilization (Lakshmanan et al., 2017).

**Elevated temperatures stress on plant growth**

High temperatures, often associated with heat shock, pose a significant abiotic challenge to both plant and microbial growth and their overall balance (Anitha et al., 2019). Identifying plant growth-promoting rhizobacteria (PGPR) strains capable of supporting plant growth at elevated temperatures has the potential to broaden the geographical range for crop cultivation, especially in anticipation of future climate scenarios. During the process of plant cold acclimation or hardening, several physiological changes are observed, including increases in sugar, proline, and anthocyanin contents. For instance, grapevine plants that have been inoculated with Bacillus phytofirmans strain PsJN exhibited higher levels of carbohydrates, proline, phenols, and displayed enhanced rates of photosynthesis and starch deposition when compared to control plants under cold stress conditions. Furthermore, the inoculation of grapevines with this PGPR strain resulted in a reduced rate of biomass reduction and decreased electrolyte leakage (a marker of cell membrane damage) during cold treatment at 4°C. It also facilitated post-chilling recovery. These findings highlight the potential of PGPRs to mitigate temperature-related stressors and their capacity to enhance plant resilience and productivity in the face of temperature challenges.

**Heavy metal contamination**

Heavy metals, including arsenic (As), chromium (Cr), cadmium (Cd), mercury (Hg), nickel (Ni) and lead (Pb), pose a significant challenge on plant and microbial growth when present at elevated levels beyond their tolerance thresholds. The toxic effects of these metals in the soil can impact the phytoremediation potential of plants. However, the application of soil bacteria can enhance phytoremediation, leading to the concept known as microbe-assisted phytoremediation. Plant growth-promoting rhizobacteria known to possess this capability represent a diverse range of genera, spanning from Alphaproteobacteria, Betaproteobacteria, and γ-proteobacteria, to Firmicutes (Shinwari et al., 2015). These microbes play a vital role in mitigating the adverse effects of heavy metal contamination (Table 6).

**Molecular mechanisms of symbiotic plant–microbe interactions**

Exploring the mechanisms driving PGPR activities holds the potential to unlock genome-editing strategies in both plants and microbes. This research aims to bolster plant growth, particularly in challenging environments. Understanding the genes, proteins, and metabolites involved in PGPR-plant interactions, responsible for conferring resistance to abiotic stress, may open avenues for engineering plants with stress-resistant genes and developing stress-alleviating microbes (Table 7).
### Table 6. Mitigating heavy metal contamination in the rhizosphere

<table>
<thead>
<tr>
<th>S. No.</th>
<th>Crop</th>
<th>PGPR</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Rice</td>
<td><em>Bacillus licheniformis</em> strain NCCP-59</td>
<td>Jamil et al., 2014</td>
</tr>
</tbody>
</table>

### Table 7. Molecular studies on alleviating abiotic stresses using PGPRs

<table>
<thead>
<tr>
<th>S. No.</th>
<th>Bacterial species</th>
<th>Plant</th>
<th>Molecular mechanism identified</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td><em>Pseudomonas fluorescens</em> FPT9601-T5</td>
<td>Arabidopsis</td>
<td>Identification of 200 genes as differently expressed in bacterial--treated plants</td>
<td>Kumar et al., 2015</td>
</tr>
<tr>
<td>2</td>
<td><em>Gluconacetobacter diazotrophicus</em> PAL5 and <em>Azospirillum</em> <em>brasiliense</em> Sp245</td>
<td>Sugarcane and rice</td>
<td>Activation the ABA dependent signaling genes conferring drought tolerance. Increase in nitrogen fixation and an increase in the expression of ethylene receptors</td>
<td>Vargas et al., 2012</td>
</tr>
<tr>
<td>3</td>
<td><em>Bacillus megaterium</em> BP17</td>
<td>Arabidopsis</td>
<td>Identification of 150 genes differentially expressed in bacterial treated plants</td>
<td>Vibhuti et al., 2017</td>
</tr>
<tr>
<td>4</td>
<td><em>Streptomyces</em> spp. viz., <em>S. diastaticus</em>, <em>S. fradiae</em>, <em>S. olivochromogenes</em>, <em>S. collinus</em>, <em>S. ossamyceticus</em> and <em>S. griseus</em></td>
<td>Chickpea</td>
<td>Increase in defense related enzymes in inoculated plants</td>
<td>Singh and Gaur, 2017</td>
</tr>
<tr>
<td>5</td>
<td><em>Dietzianatronolimnaea</em> STR1</td>
<td>Wheat</td>
<td>Confers salinity tolerance by modulating the transcriptional of salinity tolerance genes</td>
<td>Bharti et al., 2016</td>
</tr>
<tr>
<td>6</td>
<td><em>Bacillus licheniformis</em> K11</td>
<td>Pepper</td>
<td>Confers drought resistance by differential regulation of stress proteins and auxin and ACC deaminase production</td>
<td>Lim and Kim, 2013</td>
</tr>
<tr>
<td>7</td>
<td><em>Pseudomonas simiae</em> strain AU</td>
<td>Soybean</td>
<td>Facilitates induced systemic tolerance in soybean seedlings by producing a volatile organic blend</td>
<td>Vaishnav et al., 2015</td>
</tr>
<tr>
<td>8</td>
<td><em>Bacillus subtilis</em> GB03</td>
<td>Arabidopsis</td>
<td>Confers salt tolerance by regulating the Na+ transporter in by up and down regulation of HKT1 in shoots and roots</td>
<td>Zhang et al., 2019</td>
</tr>
<tr>
<td>9</td>
<td><em>Burkholderacea</em> <em>pia</em> SE4, <em>Promicromonas</em> <em>sporusc. SE188</em> and <em>Acinetobacter calcoaceticus</em> SE370</td>
<td>Cucumber</td>
<td>Confers drought and salinity tolerance in inoculated plants by reducing catalase, peroxidase; and increasing salicylic acid and gibberellin</td>
<td>Kang et al., 2014a</td>
</tr>
<tr>
<td>10</td>
<td><em>Enterobacter</em> sp. UPMR18</td>
<td>Okra</td>
<td>Salt tolerance by increasing antioxidant activity and up regulation of ROS pathway genes</td>
<td>Habib et al., 2016</td>
</tr>
<tr>
<td>11</td>
<td><em>Pseudomonas fluorescens</em> strain SS101</td>
<td>Arabidopsis</td>
<td>Results in differential up regulation of approximately 1910 genes and 50 metabolites in treated plants appose to untreated plants</td>
<td>Van de Mortel et al., 2012</td>
</tr>
</tbody>
</table>
To obtain an understanding of the physiological and biochemical alterations in the host plant Arabidopsis that resulted from the inoculation with the PGPR Pseudomonas fluorescence strain FPT9601-T5, Wang et al. (2005) employed microarray analysis. The findings demonstrated that in plants treated with bacteria, over 200 out of 22,810 Arabidopsis genes could be found to be differentially expressed (with a change of more than twofold). Most of these genes belong to functional groups such stress response, signal transduction and basic metabolism. In particular, the results demonstrated that certain ethylene-responsive genes were down-regulated while putative auxin-regulated and nodulin-like genes were up-regulated with PGPR colonization.

Gluconacetobacter diazotrophicus strain PAL5 bacterial inoculation stimulated ABA-dependent signaling genes that confer drought resistance in sugarcane, as demonstrated by Vargas et al. (2014) utilizing Illumina RNA-Seq technology. Kim et al. (2015) showed that the Bacillus subtilis strain JS volatile organic compounds (VOCs) had an impact on the gene expression profiles of tobacco. They found that plants inoculated with the PGPR strain exhibited up-regulation of tobacco genes associated with photosynthetic processes, indicating a potential VOC-mediated increase of plant growth. In addition to the gene expression profile studies previously indicated, proteomic analysis will offer more details regarding the protein or protein and pathways activated during host-PGPR interaction. Research was conducted to determine whether Bacillus amyloliquefaciens strain KPS46 could activate extracellular protein elicitors in soybean plants to promote plant development and produce systemic resistance (Buensanteai et al., 2008). Protein databases, mass spectrometry (MS) and two-dimensional polyacrylamide gel electrophoresis (2D-PAGE) were utilized to distinguish between extracellular proteins secreted by the wild-type KPS46 and the KPS46 mutant N19G1, which produces fewer extracellular proteins and does not activate growth promotion.

In the near future, advanced molecular biological techniques such as MALDI-TOF and top-down proteomics hold great promise for improved understanding of the molecular basis for plant-PGPRs interactions, despite certain limitations with using proteomic approaches to identify proteins in PGPR-plant interaction such as sample preparation issues and limited information available in protein databases (Schenk et al., 2012). Another method for analyzing the molecular mechanisms of symbiotic interactions is to profile the metabolites of both plants and bacteria. Timmusk et al. (2014), for instance, used a GC-MS approach to monitor emissions of seven stress-related volatile organic compounds (VOCs) from rhizosphere bacterially – primed drought stressed wheat seedlings. They found that three of these volatiles – benzaldehyde, β-pinene and geranyl acetone are probably good candidates for a quick and non-invasive method to measure crop drought stress.

By identifying the genes, proteins and metabolites involved in PGPRs plant interactions that underlie abiotic stress resistance, it may be possible to engineer plants with stress prevention genes and/or microorganisms that can be employed to mitigate stress.

To unlock the full potential of PGPR in agriculture, future research should focus on following aspects (Fig. 6)

1. Microbiome interactions: A deeper understanding of interactions within the microbiome is crucial to harnessing PGPR benefits effectively.
2. Molecular data: Availability of molecular data is essential for advancing our knowledge of PGPR mechanisms.
3. Stress effects: Studying the impact of environmental stresses on the microbiome and understanding the underlying mechanisms is essential.
4. Emerging technologies: Application of cutting-edge technologies like rhizo-engineering, nanotechnology, and metaproteomics can lead to more efficient and eco-friendlier PGPR formulations.
5. Formulation research: The type of formulation and its acceptance at physiological and ecological levels should be a focus area.
6. Field-scale experiments: Conducting large-scale field experiments to validate PGPR efficacy under real-world conditions is crucial.
7. Cold-tolerance: Exploring the addition of ice-nucleating plant growth-promoting rhizobacteria as a technology to enhance plant growth at low temperatures is a promising avenue for research.

Figure 6. Current and future targets for rhizosphere engineering (Ryan et al., 2009)

Challenges and future directions in harnessing PGPR benefits in agriculture

While plant growth-promoting rhizobacteria (PGPR) offer valuable advantages in agriculture, their full potential is constrained by several factors. The importance of PGPR in agriculture plays a major role. The research should aim to meet the following requirements in the future.

- Technological advancements such as meta-proteomics, nanotechnology, and rhizoengineering need to be studied in future to manufacture eco-friendly and effective inoculants.
- Developing smart biosensors allows to be studied in future to detect nutrient and contaminant levels, which enables precision farming to take place.
Nano-biofertilizers need to be encapsulated to control fertilizer transport to the target cell and avoid accidental loss.

The majority of PGPR research is carried out in a controlled setting. Therefore, research on PGPR’s field level use is necessary.

It is imperative to conduct research on the identification of microbiome interactions, their diversity, and their impact on environmental pressures, as well as their mode of action in both laboratory and field settings.

It may be possible to thoroughly study the performance of PGPR under various stress situations, such as salinity stress, temperature stress, cold stress, water logging, etc.

**Commercialization strategies**

To successfully commercialize PGPR-based products, several key factors must be considered:

1. **Cost-effectiveness**: Products must be cost-effective and offer a reasonable shelf life to be economically viable.
2. **Eco-friendly**: Eco-friendliness is a significant selling point, as sustainable and environmentally conscious products are increasingly favored.
3. **Safety database**: Availability of safety data is crucial to facilitate the registration process and ensure compliance with regulations.
4. **Educating farmers**: Farmers need comprehensive knowledge about PGPR products, including their advantages over chemical fertilizers.
5. **Changing perceptions**: Shifting farmer perceptions and attitudes toward PGPR-based products is essential for wider adoption.
6. **Training**: Farmers and field personnel should receive training on PGPR bioformulations, their benefits, and economic feasibility.
7. **Research transition**: Bridging the gap between laboratory research and practical field applications is vital for successful commercialization.

In the near future, advancements in meta-transcriptomics and meta-proteomics are expected to significantly enhance our understanding of natural PGPR populations’ activity and ecological behavior within the rhizosphere.

**Conclusion**

The global challenge of increasing crop yields while minimizing the use of fertilizer and other agricultural inputs on limited land can be addressed through rhizosphere microbial engineering. This emerging field offers exciting opportunities to fill knowledge gaps and provide solutions. This emerging field offers exciting opportunities to fill knowledge gaps and provide solutions. By exogenously introducing specific microbes or applying beneficial microbiomes on a larger scale, it is possible to modify the microbial community’s structure, enhancing stress resistance and nutrient uptake in plants. Hence, engineering of microbiomes is an essential tool for improving plants’ health, growth and functions. In order to improve our understanding of factors affecting the microbiome assemblage and its relevant feedback to a host plant, studies aiming to grasp this interplay at the community level are needed. With the support of modern tools such as “omics,” such an innovative approach can provide interesting insights.
when combined with additional efforts in rhizosphere microbiome engineering. Future research will likely leverage synthetic biology approaches, harnessing positive plant-microbiome interactions and combining various methods to boost the productivity of major food and bioenergy crops under challenging environmental conditions.

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revelation by microarray-based gene expression analysis. – J Plant Growth Regul. 36: 118.