

Rhizosphere Biology

Puneet Singh Chauhan
Shri Krishna Tewari
Sankalp Misra *Editors*

Plant-Microbe Interaction and Stress Management

 Springer

Rhizosphere Biology

Series Editor

Anil Kumar Sharma, Biological Sciences, CBSH, G.B. Pant University of
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The Series **Rhizosphere Biology**, emphasizes on the different aspects of Rhizosphere. Major increase in agricultural productivity, to meet growing food demands of human population is imperative, to survive in the future. Along with methods of crop improvement, an understanding of the rhizosphere biology, and the ways to manipulate it, could be an innovative strategy to deal with this demand of increasing productivity. This Series would provide comprehensive information for researchers, and encompass all aspects in field of rhizosphere biology. It would comprise of topics ranging from the classical studies to the most advanced application being done in the field. Rhizosphere is a dynamic environment, and a series of processes take place to create a congenial environment for plant to grow and survive. There are factors which might hamper the growth of plants, resulting in productivity loss, but, the mechanisms are not very clear. Understanding the rhizosphere is needed, in order to create opportunities for researchers to come up with robust strategies to exploit the rhizosphere for sustainable agriculture.

There are titles already available in the market in the broad area of rhizosphere biology, but there is a major lack of information as to the functions and future applications of this field. These titles have not given all the up-to-date information required by the today's researchers and therefore, this Series aims to fill out those gaps.

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Preface

The search for robust and sustainable crop production techniques is a top priority in the quickly developing sector of agriculture, where microbial interaction plays a critical role as an innovation catalyst. The interactions between plants and microorganisms are diverse and complex, ranging from mutualistic to parasitic. This book *Plant-Microbe Interaction and Stress Management* unravels the intricate mechanisms underlying the interactions between microbes and plants under stress conditions. This extensive volume provides a comprehensive examination of the applications of microbial interactions in boosting resilient plant development under a range of environmental conditions by bringing together the most recent findings, ideas, and innovations in the field.

Chapter 1 summarizes the cross-dynamics of plant–microbe interaction that can be applied in plant stress management for sustainable agricultural programs. Research on extending the shelf life of the microbial inoculum, scaling up fermentation, releasing microbes or their metabolites in the field, and bolstering legislative policies that can assist plant growth promoting microbes (PGPMs) in completing their transition from laboratory to field offer a cost-effective and environmentally beneficial method of sustainable agriculture.

Chapter 2 examines the current understanding of plant stress management when PGPM is present in unfavorable environmental settings. It also looks at the mechanism underlying the plant–PGPM interaction and how it might be applied to sustainable agriculture.

Chapter 3 highlights the ecological significance and potential of the phyllosphere microbiome in agricultural and environmental management. Understanding how microbes and plants interact in the phyllosphere makes it easier to use microbial resources to boost plant resilience and encourage ecosystem sustainability.

Chapter 4 embarks on an enlightening exploration of the impacts of waterlogging and drought on plant physiology, plant responses to climate change, and molecular pathways. Moreover, the mechanisms underlying these modifications are explained. It also explores how microorganisms that promote plant growth can enhance a plant's ability to withstand waterlogging and drought conditions.

Chapter 5 investigates the basic mechanism of plants' response to high salt concentrations and the development of effective and modern techniques for reducing salinity. It also summarizes the principal strategies for reducing the negative effects of salt on plants and provides a critical evaluation of the major advancements in this field.

Chapter 6 extends our understanding of the microbes associated with the plant's rhizosphere which play a crucial role in metal mobilization, uptake, and detoxification. Understanding plant–microbe interactions under metal stress would help in developing better agronomic and environmental practices for detoxifying metal toxicity to promote better plant growth for more productivity and environmental sustainability.

Chapter 7 lays the groundwork for creating focused and long-lasting approaches for managing bacterial diseases and supporting the vital function of both above- and below-ground beneficial biofilms. The comprehension of synergistic linkages in the plant microbiome environment and their significance for sustainable agriculture is bolstered by the insights obtained from beneficial biofilms.

Chapter 8 accentuates the important characteristics of the rhizospheric microbiome, important methods used to characterize microbial diversity, and their use in disease suppression with their mode of action. An updated knowledge framework in the field of linked rhizospheric microbiomes might be provided by analyzing the facets of the microbiome and discussing their application.

Chapter 9 provides insight into the top 10 plant viruses ranked based on their prevalence and the economic damages they inflict on their host plants. This chapter also deals with their size, shape, mode of transmission, genomic organization, replication, and movement in host cells to understand the nature of their complexity.

Chapter 10 serves as an invaluable resource for researchers and practitioners keen on leveraging insects as biotic stress in agriculture. Plants have evolved to counter the adverse effects of insects as well as to gain from them; such interaction is important for a dynamic ecosystem.

Chapter 11 discusses major antagonistic approaches toward phytopathogens emphasizing microbial biological control agents and their mode of action. In addition, this chapter also addresses the potential of microbial engineering and unravels the perspectives and possibilities of microbes as biocontrol agents, thus offering new avenues for innovation in agriculture.

Chapter 12 focuses on the cutting-edge methods and technologies that have created new opportunities for gaining a precise understanding of the interactions that occur between PGPRs and the host plant. Moreover, specific perspectives on recent technology to investigate the hitherto unknown aspect of soil microbiome have also been discussed.

Chapter 13 explores the comprehensive effects of sodic soil on soil characteristics, plant development, and the mechanisms by which bacteria promote tolerance in plants under sodic environments. Achieving the best crop production and yield under sodic stress conditions requires an understanding of the sodic environment and the mechanisms of microorganisms that promote plant growth in a sodic-tolerant manner.

Chapter 14 outlines the significance of endophytic microorganisms in comprehending plant–microbe interactions by succinctly summarizing advanced technologies and instruments for interpreting the genetic composition and ecological roles of these bacteria.

Chapter 15 concentrates on various plant biotic stressors, with a focus on fungal infections in particular. This chapter also explores the potential of exogenous administration of specific microbial agents to alleviate the detrimental effects of biotic stress on plant growth.

Throughout this book, we have included contributions from leading experts in the field, who have provided in-depth reviews of the current state of knowledge and future directions for research. We hope this book will be a valuable resource for researchers, teachers, and practitioners, fostering a deeper understanding of the intricate and mutually advantageous relationships between microorganisms and plants for sustainable agriculture.

Lastly, we would like to acknowledge the support and encouragement from the publishers, who recognized the importance of this topic and provided us with the opportunity to compile and share this valuable information with a wider audience.

Lucknow, Uttar Pradesh, India
Lucknow, Uttar Pradesh, India
Barabanki, Uttar Pradesh, India

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Chapter 1

Plant–Microbe Interaction: Stress Management for Sustainable Agriculture



Siya Kamat, Suraj Kumar Modi, Smriti Gaur, and Madhuree Kumari

Abstract The current agricultural practices demonstrate a high dependence on agrochemicals to cope up biotic and abiotic stress, which in turn results in a negative impact on environment and increases the economic burden on farmers. Plant growth-promoting microbes (PGPMs) have emerged as an eco-friendly and economic approach to combat the multiple stress faced by plants. Aboveground and belowground interactions and colonization of PGPMs can contribute to increased plant growth as well as a healthy ecosystem. Plant growth-promoting bacteria, viz. *Pseudomonas* sp., *Bacillus* sp., *Aneurinibacillus* sp., plant growth-promoting fungi, viz. *Trichoderma* sp., and plant growth-promoting actinomycetes are the most studied PGPMs in the literature used for sustainable agriculture. The main mechanisms employed by PGPMs that can be exploited for mitigating stress in plants are plant growth promotion, availability of nutrients, production of secondary metabolites, enzymes and hormones, and modulation of plant oxidative stress and plant defense. Uses of a single PGPM or the consortia of microbes have widely been reported in the literature for ameliorating plants' biotic and abiotic stress in greenhouse conditions. Despite the potential of PGPMs in sustainable agriculture, there are many hurdles that still need to be overcome. Research in sustainable release of microbes or their metabolites in the field condition, increasing shelf-life of the microbial inoculum, scaling up of fermentation, and supporting governmental policies can help the PGPMs complete their journey from lab to land and provide an eco-friendly and economic approach for sustainable agriculture.

Keywords PGPMs · Stress · Sustainable agriculture · Mechanisms · Challenges

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1.1 Introduction

Modern agriculture promises to support the food security of the rapidly growing world population. However, the agricultural practices under this modern scheme are characterized by monocultures, indiscriminate application of pesticides, chemical fertilizers—all of which contribute to nitrous oxide, greenhouse gas emission, and major biodiversity loss (Cappelli et al. 2022; Malgioglio et al. 2022). Regarding agriculture, being the backbone of several developing nations, the major challenge is to meet the food demands of the growing population within the confines of limited resources (freshwater, arable land, human labor) judiciously. Sustainable agriculture aims to meet these challenges with innovative techniques and optimize the balance between agriculture and modernity (Pandey 2018). Although sustainable agriculture is far from mainstream today, almost all countries aspire to progress toward this goal and therefore have agriculture policies in this direction. The most popular sustainable agriculture practices include permaculture (vermicompost), organic and natural farming, crop rotation, hydroponics, agroforestry, vertical farming, and integrated pest management (Gupta et al. 2021). Plant health depends on interactions with the several macro- and micro communities. While most of these practices focus aboveground, it is now established that the critical factor is plant–microbe interaction—both above and belowground (Cappelli et al. 2022; MacLaren et al. 2022). To employ microbes in sustainable agriculture, it is necessary to decipher the microbial and plant diversity, and functionality within the soil and plant microbiome. In this chapter, we aim to summarize the cross-dynamics of plant–microbe interaction that can be applied in plant stress management for sustainable agricultural programs.

1.1.1 *Plant–Microbe Interaction*

Plants and microbes interact throughout their life cycle. Spatially, the interaction occurs belowground, aboveground, and within the plant—all contributing to a healthy ecosystem. While most interactions are mediated by the plant, some occur by chance. For example, benzoxazinoids are secondary metabolites released by grasses that regulate plant health and plant–microbe integrations below- and aboveground (Cotton et al. 2019). The integration of several multiomic techniques has made it possible to investigate the beneficial plant–microbe interactions (Gamalero et al. 2022).

The spatially separated plant–microbe interactions are:

Aboveground Interaction: Microbes that colonize leaves, flowers, seeds, fruit, and stem contribute to this category. The epiphytes or phyllo-spheric microbes are influenced by the environment and therefore unstable. These microbes are often pathogenic and derive nutrition from plants. Endophytes, on the other hand, live through internal tissues through symbiosis (Nadarajah and Abdul Rahman 2021).

Chaudhry et al. (2021) summarized the properties of leaf surface and its influence on leaf-colonizing microbiota. The leaf microbiome of tomato plant could promote plant health and growth (Romero et al. 2014). Biotic and abiotic stimuli contribute to immunity priming in plant via shaping the microbial communities without much effect on plant growth. These organisms eventually trigger the host plant's basal defense and enhance resistance to phytopathogens. Microbes produce signaling molecules such as (R)- β -homoserine, β -aminobutyric acid that primes production of jasmonic acid, salicylic acid, ethylene, and brassinosteroids, thus protecting the plant from biotrophic and necrotrophic pathogens (Buswell et al. 2018). Since the aboveground microbes colonizing plants are highly adaptable to environmental fluctuations and stresses such as insects, phytopathogens, herbivores, and climate change, they represent an enormous pool of useful genetic traits.

Belowground Interaction: In plant roots, its exudates to soil, and decaying material determines the rhizospheric community or the rhizobiome. The rhizobiome in turn influences plant health, nutrient availability, and the entry or protection from pathogens. Rhizobiome is a spatial interaction that contains several bacteria and fungi drawn toward plant roots. Gu et al. (2020) investigated 80 rhizobiomes in which 2150 bacterial species [Proteobacteria (50%), Firmicutes (24%), Bacteroidetes (18%), and Actinobacteria (8%)] collectively outcompeted plant pathogen *Ralstonia solanacearum*—soilborne bacterium that causes bacterial wilt. The rhizobiome secreted siderophores—creating a competition for iron in the soil, thus suppressing competitors and protecting tomato plants. Other ways in which the rhizobiome contributes to plant health include antibiotic production, nitrogen fixation, polysaccharide degradation, and quorum sensing (Pollak and Cordero 2020).

1.1.2 The Protective Effects of Plant–Microbe Interaction

Crops are constantly exposed to a multitude of environmental stresses—biotic and abiotic. Intensive modern agricultural practices, increasing temperatures, and climate change have further aggravated loss of crops and agricultural wealth worldwide. The use of genetic engineering technologies to make resistant plant varieties is a long-term goal, and several nations do not accept these solutions. Plants in nature live with several microbial populations, and therefore, one can hypothesize that microbes can protect or help plants in biotic or abiotic stresses (Zhang et al. 2022).

In such a scenario, the use of plant microbes can be an economic strategy toward sustainable agriculture goals. Arbuscular mycorrhizal fungi and plant growth-promoting rhizobacteria have been investigated extensively for elevating plant stress tolerance and productivity (Inbaraj 2021). Figure 1.1 provides a description of how the plant–microbial communities are linked to sustainable agriculture. Plants routinely encounter abiotic and biotic stress, which can influence the microbial communities living within and around plant—above-and belowground. These stress-conditioned microbial communities have evolved to improve the plant growth

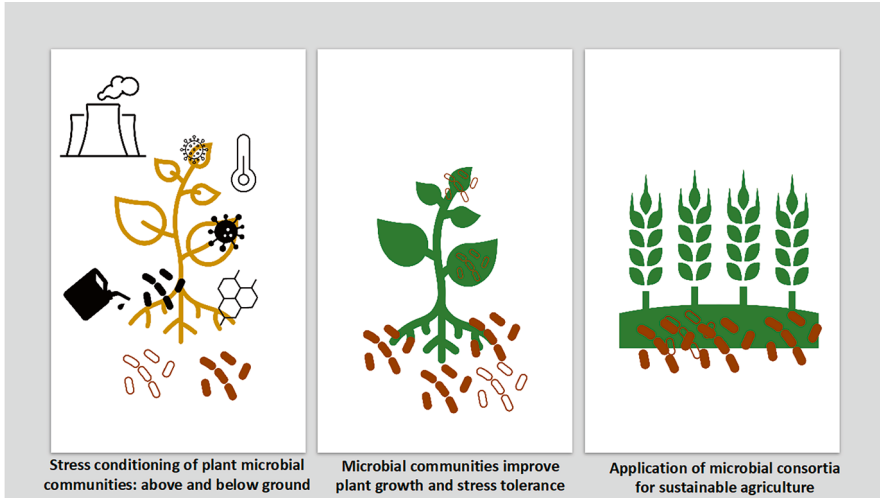


Fig. 1.1 Role of plant–microbial communities in sustainable agriculture

and stress tolerance. The application of these microbial cultures in fields can improve the productivity and provide sustainable solutions for agricultural economy.

1.1.3 Biotic Stress

Crop plants often contract pests, pathogens, and parasites, resulting in biotic stress. The infection results in vascular wilts, chlorosis, stunted growth, cankers, etc. (Hashem et al. 2019). Some examples of pathogens that cause serious diseases in crop plants are described here.

Artichoke species of the central and Mediterranean area is susceptible to several fungal infections. However, *Verticillium dahliae* Kleb. is the most infective soil-borne pathogen that causes chlorosis, stunted growth, wilting, vascular discoloration, and plant death. The microsclerotia of *V. dahlia* live in the soil for 13 years and lead to the propagation of infection through infested soil (Armengol et al. 2005). *Mycosphaerella graminicola* is a deadly fungal pathogen that causes septoria leaf blotch disease in bread and durum wheat crops (Palmer and Skinner 2002). *Pseudomonas* strains are notable for their diverse interactions with plants. One such strain is *Pseudomonas syringae* pv. *tomato* DC300 that causes bacterial infection in several plants, including tomato, and *Arabidopsis thaliana* (Worley et al. 2013). Saffron or *Crocus sativus* is an economically important crop often used as a spice, dye, and for medicinal purpose. It is often infected with fungal pathogens *Fusarium oxysporum* and *Rhizopus oryzae* causing corm rot disease (Mirghasempour et al. 2022). β -Proteobacterium *Ralstonia solanacearum* is a soilborne bacterial pathogen that causes bacterial wilt in *Capsicum annuum* L. Global warming has resulted in a

continuous spread of this infection (Lee et al. 2022). Recent studies have detected cross-pathogenic bacterial pathogens—such as *Rhizobium*, *Pantoea*, *Erwinia*, *Burkholderia*, and *Pseudomonas*—that can cause infections in plants and animals/humans (Kizheva et al. 2022). Necrotrophic fungus *Botrytis cinerea* is a deadly pathogen that infects postharvest pepper fruit and causes gray mold, leading to huge economic losses (Wang et al. 2022). Apple plants are often infected with *Colletotrichum* species (*C. alienum*, *C. fructicola*, *C. gloeosporioides sensu stricto*, *C. nymphaeae*, *C. siamense*, and one new species, *C. orientalis*) (Chen et al. 2022). In a recent study, new pathogenic fungal strains *Neofusicoccum australe*, *N. crypto australe/stellenboschiana*, *N. luteum*, *N. parvum*, and *Lasiodiplodia brasiliensis* were detected that cause dieback and stem-end rot diseases in avocado plants in the Canary Islands of Spain (Hernández et al. 2023).

1.1.4 Abiotic Stress

While a lot is discussed about the biotic stress and abiotic stress individually, very little is known about how abiotic stress affects the plant's ability to combat infections or how stress changes the plant's microbiome. Bhandari et al. (2023) studied the effect of elevated tropospheric ozone (O₃)—alone and in combination with a bacterial infection (*Xanthomonas perforans*)—on susceptible and resistant varieties of pepper cultivars, and their associated microbiome. It was observed that O₃ stress elevated the severity of *X. perforans* infection only in the resistant pepper cultivar. This was due to the dramatic shift in the microbiome structure, which indicates that the microbial communities respond distinctly to biotic and abiotic stress. The endophytic fungi of wheat plants sampled from North China could protect the host wheat plant from several abiotic stresses such as drought, temperature tolerant, salinity, and heavy metal and could promote plant growth. Tomato plants are severely affected due to saline soils and quality of irrigation methods, both of which result in considerable produce losses. Muthuraja and Muthukumar (2022) sampled non-mycorrhizal bacteria—*Aspergillus violaceofuscus* and *Bacillus licheniformis* from saxicolous habitat—and proved the usage of this coculture to withstand salinity and promote growth in tomato plants. In another study, microbial consortium comprised of *Enterobacter* sp., *Bacillus* sp., *Achromobacter* sp., and *Delftia* sp. could alleviate salinity stress and promote growth of tomato plants (Kapadia et al. 2021). Jiao et al. (2016) discovered melatonin-producing endophytic bacterium, *B. amyloliquefaciens* SB-9, from grapevine roots. The endophyte colonization and melatonin production could counteract the abiotic stress—salt and drought—protecting and promoting the growth of grapevine. Plant growth-promoting fungi are also investigated as inducers of heavy metal detoxification by seed priming and biofortification (Geetha et al. 2023).

1.2 Plant–Microbe Interaction Can Mitigate Biotic and Abiotic Stress

Plant interaction with the microbial life is a diverse ecosystem wherein different interactions occur: symbiosis, mutualism, parasitic, etc. Plant microbiome—which includes endophytes, plant growth-promoting rhizobia, and mycorrhizal fungi—is capable of alleviating the biotic and abiotic stress and improve plant growth. These microorganisms are critical players of plants' defense and well-being. Therefore, they offer sustainable solutions to increase agricultural productivity (Munir et al. 2022). Table 1.1 describes recent examples of the potential use of microbes in mitigating biotic and abiotic stress in plants.

1.3 Mechanisms Employed by Plants for Overcoming Stress

Plants have evolved and acquired immense mechanisms to tackle, avoid, and encounter several biotic and abiotic stresses. Failing to have proper strategies can threaten the survival of plants and essentially affect the productivity of plants and crops. Plants are known to establish symbiotic relationships with multiple microbes, which protect and profit from each other in multiple ways. The key strategies and mechanisms evolved by the plant species for stress management are the following.

1.3.1 *Plant Growth Promotion*

Plants have established symbiotic relationships with various microbes to tackle biotic and abiotic stress followed by promoting sustainable strategies. For example, plant growth-promoting rhizobacteria (PGPR) is one of the most common and important plant-associated bacteria that have been extensively utilized as it promotes plant growth and promises sustainable agriculture. Additionally, it enhances plant–microbe interaction with a nominal adverse effect on the soil microbiota. Studies have shown that phytohormone melatonin produced by the native PGPR enhances the tolerance potential of plants from various biotic and abiotic stress. Jofre et al. (2023) evaluated the production of melatonin by two native PGPR bacteria *Enterobacter* 64S1 and *Pseudomonas* 42P4 in the *Arabidopsis thaliana* plant. Moreover, these two bacteria could enhance endogenous melatonin content even when *Arabidopsis thaliana* was exposed to grow under drought conditions. Mechanistic analysis suggested that these PGPR native strains could enhance the tolerance level of plants in drought by preventing membrane damage, and oxidative stress, and ultimately promoting plant growth (Jofre et al. 2023). Besides rhizobacteria, several other endophytic bacterial species play a critical role in providing

Table 1.1 Recent examples of the potential use of microbes in mitigating biotic and abiotic stress in plants

Biotic stress			
Pathogen	Host plant	Plant growth-promoting microbe	Reference
<i>Fusarium</i> spp.	Saffron	<i>P. Aeruginosa</i> YY322	Mirghasempour et al. (2022)
<i>Botryosphaeria dothidea</i>	Apple plant	<i>Bacillus amyloliquefaciens</i> FX2	Li et al. (2022a, b)
<i>Blumeria graminis</i>	<i>Achnatherum inebrians</i>	<i>Epichloë</i> endophyte	Zhu et al. (2022)
<i>Fusarium oxysporum</i>	Tomato	Endophyte: <i>Beauveria bassiana</i>	Nchu et al. (2022)
Fungal pathogens: <i>Fusarium oxysporum</i> f.sp. <i>cicero</i> , <i>Rhizoctonia solani</i> , <i>Sclerotium rolfsii</i>	Chickpea	<i>Bacillus subtilis</i>	Mageshwaran et al. (2022)
<i>Golovinomyces cichoracearum</i> : Powdery mildew disease	Tobacco	<i>Seimatosporium</i> sp. M7SB41	Zhao et al. (2023)
<i>Fusarium oxysporum</i> , <i>Rhizoctonia solani</i> , <i>Pythium aphanidermatum</i>	<i>Pisum sativum</i>	Endophytes isolated from <i>Ocimum sanctum</i> Linn: <i>Pseudomonas aeruginosa</i> OS_12, <i>Aneurinibacillus aneurinilyticus</i> OS_25	Gupta et al. (2022)
Abiotic stress			
Stress	Host plant	Plant growth-promoting microbe	Reference
Salinity	<i>Hibiscus hamabo</i>	Arbuscular mycorrhizal fungi	Yuan et al. (2019)
Heavy metals, salinity, drought, and temperature	Wheat	Wheat endophytic fungi: <i>Trichoderma</i> strains	Ripa et al. (2019)
Salinity	Tomato	<i>Bacillus spizizenii</i> FMH ₄₅	Masmoudi et al. (2021)
Salinity	Tomato	Co-inoculation: <i>Bacillus licheniformis</i> and <i>Aspergillus violaceofuscus</i>	Muthuraja and Muthukumar (2022)
Salinity and drought	Grapevine	<i>Bacillus amyloliquefaciens</i> SB-9	Jiao et al. (2016)
Metal stress	Soyabean	Plant growth-promoting rhizobacteria— <i>Acinetobacter beijerinckii</i> and <i>Raoultella planticola</i>	Hussain et al. (2023)

resources and nutrients needed for plant growth, thus promoting plant growth and modulating the development of plants (Ma et al. 2016; Santoyo et al. 2016).

1.3.2 Root Colonization and Availability of Nutrients

Plant roots are one of the best parts for colonization as they remain exposed to soil and offer a wide range of interaction and inhabiting soil microorganisms including the rhizosphere (Saeed et al. 2021). Synek et al. (2021) showed the colonization and inhabiting of endophyte *Enterobacter* sp. SA187 in various plants, including, wheat, barley, and *Arabidopsis*. Essentially, this helps in plant growth and strengthen plant-tolerating potential under an unfavorable environment (Synek et al. 2021). Many bacterial colonization offer the availability of essential nutrients and supplements required for plant growth and utility. PGPR colonizes the rhizosphere of an agronomically important crop *Azospirillum brasilense*, followed by modulating the root architecture and enhancing the bioavailability of nutrients (Pii et al. 2015). Another recent study demonstrated that *Pseudomonas putida* KT2440 is an excellent root colonizer when colonized soybean and corn plants resulted in enhanced seed germination and stem length under elevated saline conditions compared with uninoculated plant (Costa-Gutierrez et al. 2020).

1.3.3 Secretion of Phytohormones and Enzymes

Plants survival under biotic and abiotic stress becomes feasible as the symbiotic association of plants with microbes helps not only in their growth but also provides protection from different phytopathogens, including infectious bacteria, fungi, and viruses. Mechanistically symbiotic bacteria and PGPR induce secretion of phytohormones and upregulated enzymes required by plants for their overall development. For example, *Bacillus subtilis* is well known for playing a significant role in improving tolerance potential to biotic stresses. Moreover, it degrades the precursor of ethylene ACC and helps plants grow and maintain their normal growth under stressful conditions (Glick et al. 2007; Hashem et al. 2019). Additionally, *Bacillus* spp. is also known to secrete siderophore exopolysaccharides that downregulate the movement of toxic ions and hence maintain the ionic balance. Interestingly, it enhances the water transportation across plant tissues and essentially protect from pathogenic microbes (Radhakrishnan et al. 2017). *Bacillus subtilis* possess chemoreceptors that enable them to recognize the right environment to interact.

1.3.4 Secretion of Secondary Metabolites and Volatile Organic Compounds

Plants produce a wide range of secondary metabolites and volatile organic compounds in response to the stress caused due to biotic and abiotic factors. Environmental factors, including humidity, temperature, and CO₂ content, can influence the production of secondary metabolite production. Certain environmental conditions, including high salinity, freezing temperature, drought, and mineral content in soil, essentially can cause adverse effects on plants. However, various volatile organic compounds and secondary metabolites encounter the adversity and allow them not only to stand but also maintain homeostasis (Ramakrishna and Ravishankar 2011).

Phytoalexins are one of the secondary metabolites usually present in trace amounts in healthy orchids, and when they are exposed to pathogenic fungi they significantly upregulate the genes encoding phytoalexin enzymes (Reinecke and Kindl 1994). Similarly, terpenes have multiple functions in plants, including protection against various phytopathogens and herbivores. As per previous studies, hemiterpenes enhance thermotolerance and photosynthesis rate in some of the plant species. Moreover, it has been demonstrated that when oak (*Quercus ilex*) leaves are fumigated with monoterpenes, they enhance the thermotolerance of the plant (Bartwal et al. 2013). Snowdrop lectin produced in *Triticum aestivum*, *Oryza sativa*, and *Arabidopsis* spp. potentially works as insecticidal for insects, including *Nilaparvata lugens*, Aphids, *Pieris rapae*, and *Spodoptera littoralis* (Saha et al. 2006). There are many more secondary metabolites known to protect plants and promote their growth and play a crucial role in maintaining homeostasis (Al-Khayri et al. 2023).

1.3.5 Reduces Oxidative Stress

A plant's ability to respond to the extreme stress condition is considered a crucial function. Understanding plant's strategies for tackling oxidative stress is important as it significantly regulates the plant's health and development. Several environmental factors, including UV stress, herbicide action, pathogens invasion (hypersensitive reactions), and unavailability of enough oxygen, can induce oxidative stress in plants. Besides environmental factors, plant's developmental transitions such as seed maturation induce reactive oxygen species (ROS). However, plants have evolved themselves and defensively act against ROS by activating genes associated with antioxidant molecule synthesis. Several studies have reported that chloroplast and peroxisomes are more prone and attacked by ROS (Grene 2002; Blokhina et al. 2003; Saha et al. 2006; Al-Khayri et al. 2023). To neutralize the effect of ROS and their effect, plants respond with upregulated synthesis of certain enzymes, including

superoxidase, monodehydroascorbate reductase, and ascorbate peroxidase (Mullineaux et al. 2000).

1.3.6 Modulation of Plant Defense System

Plants are subjected to a plethora of foreign invaders throughout life that potentially impact their health and productivity. However, long exposure to such invaders allows plants to modulate their immune system and resist and respond against pathogens. Plant's first line of defense are equipped with pattern recognition receptor that potentially identify pathogen-associated marker patterns (PAMPs), known as PAMPs-triggered immunity (PTI) (Monaghan and Zipfel 2012). Moreover, plants are also acquired for the rapid and transient perturbations of calcium ion (Ca^{2+}) concentration, which activate a set of gene activation to generate requisite response to invaders (Reddy et al. 2011). Additionally, in response to the biotic stresses or invasion, PTI stimulate the expression of Ca^{2+} ion channels, resulting in an increase in cytoplasmic Ca^{2+} concentration and ultimately make an unfavorable environment to survive the pathogens and invaders.

1.4 Process of Microbial Inoculation: From Lab to Land

Environmental stresses, including biotic and abiotic factors, directly impact the productivity of plants and crops. Therefore, it has been imperative to develop strategies that can globally increase the plants' utility and enhance the agricultural food productivity in more economical and sustainable ways (Lopes et al. 2021). Besides limiting the exposure to chemical fertilizers, pesticides, and insecticides, it is also important to plan and uplift the idea of using beneficial microorganism and colonizing and integrating them with plant system to not only reduce the exposure to toxic and harmful chemical to the environment but also be ecofriendly, a sustainable approach to enhance the crops' productivity (Khan et al. 2020). Extreme environment can be a good source for selecting, isolating, and utilizing the beneficial microorganisms. For example, Inostroza et al. (2017) showed that microbial consortia taken from the rhizosphere of *Atriplex* sp., when grown in soil with undisturbed arid Chilean ecosystem, followed by wheat seedling result in the enhanced growth even in dry soil with limited phosphorus content (Inostroza et al. 2017). Environments like halophytic area can be a potent source for identifying beneficial microorganisms (Salwan et al. 2019). An exhaustive study by Mayak et al. (2004) led to the finding of 115 endophytes isolates from different crop wild relative (CWR) halophytes, which includes *Matthiola tricuspidata*, *Cakile maritima*, and *Crithmum maritimum*. Interestingly, many of the strains prevent the invasion of phytopathogens and a few were also acting as an antagonist for human pathogens like *Aspergillus fumigatus* (Mayak et al. 2004). Furthermore, some of the strains

complemented with enhanced plant growth and uplifted salinity tolerance. Studies have also reported several other microorganisms associated with PGPM such as *Azospirillum*, *Bacillus*, *Enterobacter*, *Burkholderia*, *Flavobacterium*, *Clostridium*, *Pseudomonas*, *Frankia*, *Trichoderma*, and *Rhizobium* that have efficiently played imperative roles toward establishing a sustainable agriculture and improved plant productivity (Abhilash et al. 2016; Van Oosten et al. 2017; Gouda et al. 2018). These PGPM establish a symbiotic relationship with plants and help them by modulating phytohormone production, enhancing nutrient availability of soil and acting as barriers to pathogens (Asghari et al. 2020). Moreover, it can be colonized through different inoculation methods, including roots, soil, and foliar inoculation, which will have adequate interaction between plants and microorganisms. Among these methods, seed inoculations are the most common while foliar is the least. Interestingly, seed inoculation method is potentially used as an alternative to chemical treatment. Seed inoculation implies the immersing of the seed in microbial solution of known concentration (Lopes et al. 2018). The seed germination process provides abundant amino acids and carbohydrates in the form of seed exudates (Ahemad and Kibret 2014). Associated microorganisms utilize them as a source of nutrients and colonize and emerge into them when inoculated seed get transferred into the soil (Ammor et al. 2008). A study showed that seed inoculation with *Rhizobial* and *Bacillus* sp. enhanced the biomass production of *Cicer arietinum* (Khan et al. 2019) and *Oryza sativa* (Ullah et al. 2017), respectively. Another similar study reported that seed inoculation with *Burkholderia phytofirmans* led to enhanced phytoremediation of organic pollutants, including hydrocarbons (Afzal et al. 2013). Similarly, *Pseudomonas fluorescens* essentially increase the vigor biomass and enhance the resistance potential to water stress of *Virgin radiate* (Saravanakumar 2012).

Like seed inoculation, root inoculation method implies immersing roots in a microorganism solution. Post inoculation, seedling is planted to proper substrate and allowing size standardization. Additional advantages of this method are that inoculum is directly exposed to the host root and improves root colonization. Studies have shown that in plant species with asexual propagation, PGPM inoculated through the root method could show the enhanced ability of phytohormone synthesis such as auxin. Moreover, it also showed preventive activities against phytopathogens (Ahemad and Kibret 2014; Gouda et al. 2018). A study demonstrated that root inoculation with *Burkholderia* sp. enhanced *Vitis vinifera plant* growth and yield by elevating the tolerance level tolerance to low-temperature, modified carbohydrate metabolism (Fernandez et al. 2012). Another method of inoculation is soil inoculation, where PGPM are directly introduced into the soil by drenching, soil incorporation (mixed in the substrate), or microcapsule (Lopes et al. 2018). A study by Li et al. (2022a, b) demonstrated that when soil was inoculated with *Bacillus* it resulted in better nodulation and growth of *Cicer arietinum* (Li et al. 2022a, b). Another study by Hernandez-Montiel (2017) showed that the growth and productivity of *Lycopersicon esculentum* were significantly enhanced when soil was inoculated using *Pseudomonas putida* incorporated into the microcapsule (Hernández-Montiel et al. 2017). Additional advantages of delivering *Pseudomonas putida* in

microcapsule are gradual release, greater viability, protection, and stability of roots. These results suggest that the inoculation method essentially influences the growth of plants and productivity of crops when beneficial microorganisms are utilized in a certain way.

The basic roadmap to the commercialization of PGPRs is not stringently specified but includes the basic orderly guidelines (Backer et al. 2018):

- (a) Extraction of the bacterial species from the plant.
- (b) Growth and screening of the microbes (single or multiple).
- (c) Selection of the appropriate field for the growth of the crop within a certain environmental frame.
- (d) Trail and testing of the best possible combinations of the bacterial strains.
- (e) Planning of the prime field management applications.
- (f) Purification of the final product.
- (g) Checking the toxicity effects.
- (h) Analysis of the finest form of delivery of the product.
- (i) Ethical and regulatory approvals.
- (j) Marketing of the product.

To formulate PGPR-based products, the composition should be such that it allows even dispersal in the field such as inoculums in the legume industry are mainly subjected to solid-based carriers, for example, sterilized peat (Bashan et al. 2014). This carrier system includes the inoculated cells, which are stuck to the surface of the seed during sowing in the field. Alternatively, alginate-based solid carriers have also been used due to sustainability issues of the peat (Bashan 2016). Other sources as potential candidates include biochar due to the flexibility to alter the nutrient and porous nature of the material (Głodowska et al. 2016).

1.5 Challenges, Limitations, and Future Perspective

Agriculture sector has been thriving over the years with the enormous use of chemical fertilizers and pesticides, which has led to a steep increase in the destruction of good soil microflora, causing detrimental effects to the environment as well as to the farmers. In search for the production of the beneficial crop, recent methods focus on the plant–microbe interaction to improve the yield and variety of the crop plants. The good microbes produce certain phytohormones, including auxins, gibberellins, abscisic acid, and cytokinins (Fahad et al. 2015). PGPMs can prove to be good alternatives that can strengthen the rhizosphere of the plants by naturally secreting the organic compounds and certain growth hormones required for viability of plant tissues. The plant–microbe symbiosis is triggered by the secretion and stimulation of favorable compounds required for plant growth. The major microbes benefiting the soil rhizosphere include *Pseudomonas* sp., *Bacillus* sp., *Rhizobium* sp., *Klebsiella*, and *Clostridium* sp., amongst others (Abhilash et al. 2016; Gouda et al. 2018; Van Oosten et al. 2017).

However, one of the major challenges faced by the overall composition of the rhizomicrobiome is the continued growth and maintenance of the live bacterial cells, that is, their shelf life. Studies report that the spore-forming Gram-positive bacteria maintain longer shelf life than the Gram-negative bacterial species (Schoebitz et al. 2013). Also, a big challenge is to eradicate the crosstalk between different bacterial species, which may lead to the development of biofilms (Ajijah et al. 2023; Karimi et al. 2022). Some of the interspecies interactions may prove to be fatal due to the matrix forming proteins and enzymes. Moreover, studies report the pathogenicity of a few microbial species like *Pseudomonas* sp. and *Burkholderia* sp. to humans (Kumar et al. 2013). The plant–microbe interaction serves as a mutual relationship, with the plant serving as a nutrient source and the microbes enhancing the growth of the plant. However, environmental changes play an important role in maintaining this plant–microbe interaction. The humid conditions within the soil and the extreme temperature fluctuations due to heat or cold and salinity make it difficult for the microbial inoculum to grow and proliferate (Bailey-Serres et al. 2019). Also, the other limitation is that the plants are exposed to pest attacks, which when healed are most likely to re-emerge due to climate changes. The constant climate changes have limited the yield from plants, leading to the adaptation of more synthetic ways for a highly viable crop production (Moore et al. 2017). The strategies to enhance the resilience and sustainable growth of plants will be beneficial with their localized implementation in agriculture fields.

Studies have proven to be impactful in using PGPMs as a method to safeguard the ecosystem by reducing the usage of chemicals and improving the productivity of the plants. Certain PGPRs, including that of *Pseudomonas*, *Rhizobium*, and *Azotobacter* species, amongst others, are being utilized commercially for large-scale production (Parray et al. 2016). Other approaches to enhance the utility and mass production of PGPRs are by modulating their usage through new technologies. Nanoparticle bead encapsulation is being done for the refinement of PGPRs (de Moraes et al. 2021; Nayana et al. 2020). The microbiome of the plant seeds can be modulated by using the microbial inoculation within the seeds for enhancement of the plant growth (Mitter et al. 2017). Future studies can be directed toward the use of microbial consortium with many advantages. Certain plant microbes can help provide essential nutrients to the plant growth and improve the fertility of the soil. The microbes used as PGPRs can also act as decomposers of toxic waste and help in getting rid of the accumulation of harmful waste products. These PGPRs can also be beneficial by supplementing the plant system with vital products that may help boost the immunity of the plants. Another important aspect could be the shielding effect from the environmental stresses. The future holds promise in the field of crop improvement with the help of plant growth-promoting microbes. However, economical techniques using microbes for more effective utilization by the farmers are needed. The manufacturers can include government-aided norms for regular and timely delivery of a fresh bacterial slot with higher stability and shelf life (Bailey-Serres et al. 2019). Also, proper guidelines and training can be given to the farmers by the communal administration to use the biofertilizers, including microbes, effectively. The government initiatives to help localize the use of microbes by

small-scale setups by the farmers can help them maintain a systematic and consistent production of the inoculum (Vishwakarma et al. 2020). These measures can certainly assist in improving cell viability and stability of the bacterial inoculum to be used in the future.

1.6 Conclusions

With a continuously increasing population and climate change, there is an urgent need to search for sustainable substitutes for agrochemicals. Biofertilizers and biopesticides are eco-friendly and economic alternatives to toxic chemicals for stress management and plant growth promotion. Despite some limitations, research should be focused on the effective and timely transition of PGPMs from lab to land for stress management in sustainable agriculture.

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