

Rhizosphere Biology

Suresh Kumar Dubey
Satish Kumar Verma *Editors*

Plant, Soil and Microbes in Tropical Ecosystems



Springer

Rhizosphere Biology

Series Editor

Anil Kumar Sharma, Biological Sciences, CBSH, G.B. Pant University of Agriculture & Technology, Pantnagar, Uttarakhand, India

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Foreword

The concept of rhizosphere was enunciated by Hiltner in 1904. Rhizosphere biology per se takes into its ambit organisms that belong to large groups of bacteria, fungi, Protozoa, nematodes, and insects. Thus it is interactions in this complex milieu that are to be considered critically in order to arrive at any meaningful conclusions. This inter alia requires that rhizosphere is analysed not only at a single plant level but also at field scale. Available information derived from laboratory and field investigations suggests complexity not only at species level but also at population and community scale. Until recently this information was derived for especially bacteria and fungi through phenotypic studies based on artificial media and the data so generated was therefore difficult to duplicate for a single soil site. This situation has now completely changed with the availability of tools of metagenomics and gene sequencing, which permit exploration of microbes that were prone to artificial cultivation. As a result it is possible now to investigate rhizosphere into its variable components not only into species spectrum but also at temporal and spatial scales. In addition, the availability of other advanced analytical tools including microscopes allows deeper investigations into the realm of in situ localization of microbial communities and diffusivity of nutrients from nutrients that play an important role in interactions that are pivotal to appreciate the close linkages between below ground and above ground components of the plant ecosystem. It is the music generated in the rhizosphere that culminates in improved shoot growth with the resultant better plant productivity. Notwithstanding these attributes, rhizospheric microbial populations are an admixture of neutral, antagonistic, mutualistic, and pathogenic components. Any disturbance by way of use of herbicides and pesticides can disturb the delicate equilibrium that may take long to come back to normalcy. Among these inhabitants, mutualists belonging to the group mycorrhizae extend their hyphae as additional root hairs and thus exert a “mycorrhizospheric” effect. On the other hand nodules in case of leguminous crops are a harbinger of non-nitrogen fixing yet growth promoting bacteria with further influence of the rhizosphere of plants. The inter-linkages of phosphorous and nitrogen economy come to play a decisive influence through these two groups of mutualists with resultant beneficial influence

on crop productivity. In tropical ecosystems the role of nutrient turnover can make or mar the survival and fitness of a plant community under such circumstances. Considering limitations and desirability of sustained production systems to meet the food demands of tomorrow, bringing together published information on the subject is always a welcome step. In the present volume, the editors, Prof. S.K. Dubey and Dr. S. K. Verma, have done a useful exercise to fill this gap. I hope it will further the cause of rhizosphere biological assessment with tomorrow's needs and aspirations.

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Preface

Microbial communities have a profound effect on the performance of plants by influencing their growth and development. Plant-associated microbes including mainly archaea, bacteria, and fungi are beneficial as well as harmful to them. Large proportions of these microbes live in the close vicinity of the roots (rhizosphere) and are called rhizospheric microorganism. Actually, plants selectively recruit soil microbes towards the rhizospheric region to get benefits in terms of nutrient acquisition, growth stimulation, and protection from biotic and abiotic stresses. The composition of these rhizospheric microbial communities and the level of interactions with plants largely depend on the type of soils, plant genotype, and abiotic factors. Some of the microbes including endophytes, rhizobia, and mycorrhizae enter into the root tissues and develop permanent internal mutualistic association. Rhizospheric microorganisms and mycorrhizae have been well studied for their beneficial role in plant development and protection. They improve host plant fitness by mobilising inorganic nutrients such as nitrogen, phosphorus, potassium, and iron, fixing atmospheric nitrogen, producing growth hormones, and suppressing plant pathogens. Also they induce host plant gene expression for better adaptation. Excessive and injudicious use of chemical fertilisers and pesticides already has impacted our ecosystems, posing a great threat to human and animal health. Also these chemicals disturb the composition and interactions of natural microbiota. Research and knowledge of rhizospheric biology would be very critical in manipulating rhizospheric microbes for making strategy for sustainable cultivation of crops and medicinal plants. Nevertheless, a majority of the microbes is non-cultivable and hence new technological approaches such as functional metagenomics and high-throughput sequencing need to be designed to understand better the functional role of non-cultivable microbes. Most of the studies related to plant–microbe interactions pertain to temperate regions despite the fact that tropical ecosystems are richer in diversity and are complex in terms of plant–microbe interactions. It is very crucial to develop a better understanding of how the soil types and abiotic factors influence the plant–soil–microbe interactions in tropics. In view of the aforementioned issues, this volume in the “Rhizosphere Biology” series

is titled *Plant, Soil and Microbes in Tropical Ecosystems* to cover the research topics related to tropical ecosystem rhizosphere–microbial interactions.

This volume consists of 17 chapters in which we covered areas ranging from application and development of modern techniques and tools to study rhizospheric biology to basic science and research development, understanding diversity and functional roles, and application of rhizospheric microbiota in developing new alternative technology, i.e., biofertilisers and biocontrol agents for sustainable agriculture.

In this book, attempts have been made to highlight multi-dimensional plant–microbe interactions in tropical agroecosystems. This book provides a glimpse of the basic and advanced perspective towards rhizospheric biology designed for a wide group of readers.

We have great pleasure in bringing this book to a global audience. We express our sincere gratitude to all the contributors for significant contributions towards the completion of this volume. We are also grateful to reviewers for improving the quality of the chapters included in this book. We also thank Ms. Madurima Kahali, Ms. Vaishnavi Venkatesh, and the entire production team at Springer for their cooperation and support in bringing out this book.

Varanasi, Uttar Pradesh, India

Suresh Kumar Dubey
Satish Kumar Verma

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About the Editors



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and edited a book on *Seed Endophytes*. His areas of research interest include the functions of plant microbiomes, diversity and ecology, and the roles of microbes in the modulation of plant development and protection of hosts from biotic and abiotic stresses.

Chapter 1

Plant–Rhizobacteria Interactions to Induce Biotic and Abiotic Stress Tolerance in Plants



Raghvendra Saxena, Manish Kumar, and Rajesh Singh Tomar

Abstract Climate change and extreme environmental conditions are recognized as the most challenging threats to agricultural systems, leading to significant limitations in crop production and yield worldwide. It is a big concern to increase or maintain crop productivity under changing climate conditions to cater for increasing food demand. Among abiotic stresses, salinity, drought and extreme heat are the most common stresses. Abiotic stresses contribute to reducing crop plant production by 50% or more. Like the effects of abiotic stress, constant exposure to biotic stresses—which include pathogen infections and pest and insect attacks—contribute to a major drop in crop productivity and wastage of crops. There is also constant pressure from extreme weather conditions due to climate change and the incidence of biotic stresses. There is a great need to develop biotic and abiotic stress resilience in crops to mitigate the adverse effects of stresses. Such resilience can be achieved through development and adoption of eco-friendly approaches in agricultural systems for crop sustainability and food security. The focus on plant–microbe interactions has attracted more attention in recent years for inducing plant resistance and defence against abiotic and biotic stresses. Plant growth–promoting rhizobacteria facilitate abiotic stress resilience in plants by several strategies through activation of plant growth regulators (which include ethylene, auxin (indole-3-acetic acid)), activity of enzymes such as 1-aminocyclopropane-1-carboxylate (ACC)–deaminase and production of bacterial products such as exopolysaccharide. Diverse plant–microbe interactions in the rhizosphere also help to regulate plant defence pathways under adverse conditions through induction of systematic resistance or systemic acquired resistance. Moreover, other strategies such as microbial antagonism through production of several compounds such as antibiotics, siderophores, bacteriocins and secondary metabolites further boost disease resistance in plants.

Understanding of the great importance of plant growth–promoting rhizobacteria in agricultural systems and their involvement in induction of plant defence

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mechanisms through various strategies to increase crop resilience against adverse conditions offers a potential tool to maintain sustainability in agricultural systems.

This chapter focuses on the role of plant–microbe interactions and application of plant growth–promoting rhizobacteria to attain comprehensive protection of crops in adverse conditions to address crop sustainability and food security.

Keywords Biotic stress · Abiotic stress · PGPR · Induced systematic resistance (ISR) · Systemic acquired resistance (SAR)

1.1 Introduction

Abiotic and biotic stresses affect plants and animals. Being sessile organisms, plants are greatly affected by these stresses and environmental changes because they cannot escape from these adverse situations and must instead tolerate them. Therefore, perturbations of external environmental conditions that negatively affect plants' physiological and metabolic activities lead to limitations in growth and development. Moreover, such stresses induce several adaptive responses in plants at the cellular and molecular levels to mitigate adverse effects of plant pathogens and environmental stresses (Verma et al. 2013). Extreme environmental conditions and pathogen attacks are important causes of negative effects on crop productivity worldwide (Grover et al. 2011).

With growth in the human population and inflating food demand, food security and production have become major challenges in the current agricultural scenario worldwide. It is estimated that 70% more food crop production will be required to fulfil the food demands of 2.3 billion additional people by 2050 globally (FAO 2009).

Plants are frequently exposed to adverse environmental conditions and consequently experience poor growth and productivity. These environmental stresses are broadly categorized into two groups: biotic stresses and abiotic stresses. Abiotic stresses—salinity, desiccation, high temperatures, floods, cold, heavy metal contamination etc.—put major constraints on crop growth and productivity worldwide. Among abiotic stresses, drought, salinity and extreme temperatures are major stresses that cause huge losses of crop productivity globally because of their adverse impacts on growth, development, yield and seed quality of crop plants. In a wide variety of crops, abiotic stresses result in yield losses ranging from 10% to 50% or more, depending on the crop (Gull et al. 2019). Drought, salinity and extreme temperatures are among the most important abiotic stresses. It was previously estimated that approximately 1.8 billion people would face acute freshwater scarcity in the first quarter of the twenty-first century, while the rest of the population would face water crises to a considerable extent (Nezhadahmadi et al. 2013). Abiotic stresses, especially drought and salinity, are known to cause major reductions in crop yields and economic losses to farmers. Increasing climate change and

recurrence of abiotic stresses are major threats to food security and sustainability of crop production systems.

Plant responses to abiotic and biotic stresses are intricate phenomena, governed by multiple complex traits. Therefore, it is important to understand plants' responses and their underlying mechanisms under adverse conditions in order to enhance plant resistance, which is the major concern in the current agricultural scenario (Saxena et al. 2019a, b; Raza et al. 2019).

Abiotic stresses are mainly governed by perturbations in nonliving components of the environment, whereas biotic stresses are those imposed on plants by a wide variety of other organisms, including viruses, fungi, insects, pests, nematodes, arachnids, weeds etc. These organisms' attacks on crop plants cause adverse impacts on the plants by depriving them of nutrients or by changing their physiological and metabolic activities, resulting in poor growth and less development. Moreover, under extreme and severe conditions, they may kill the plants. Biotic and abiotic stresses also severely affect crop productivity and cause major crop losses. Plants do not possess an immune system; therefore, they have evolved various defence strategies governed by their genetic composition to prevent deleterious effects of pathogen attacks (Gull et al. 2019; Verma et al. 2016). Plant–microbe interactions play important roles in strengthening plant defences against abiotic and biotic stresses. Interactions with nonpathogenic bacteria are important in providing effective tolerance or bioprotection against biotic stresses in plants when they are inoculated; similarly, interactions with root-colonizing bacteria enhance abiotic stress tolerance in plants. There is a need to address the issues of abiotic and biotic stresses associated with crop loss by identifying strategies and technological approaches that can promote crop resilience under adverse conditions and help mitigate the adverse effects of those stresses. Further, such approaches should be environmentally friendly and should not require large expenditure. They should be based on promoting adaptations in plant capacity under stressful conditions (Kang et al. 2009).

Microorganisms constitute the most vital component of the earth's living system, since microorganisms are the natural inhabitants of the soil and thus a vital living component of the rhizosphere. Plant–microbe interactions constitute the most delicate system in the agricultural system that contributes directly or indirectly to agricultural crop production. Moreover, microbes contribute to seed germination and growth as natural inhabitants in various symbiotic associations (Chakraborty et al. 2015). Different types of plant–microbe interactions constitute an important component of the ecosystem, and such plant–microbe interactions regulate plant defence mechanisms for better survival under extreme conditions (Kumar et al. 2019; Meena et al. 2017).

Soil microorganisms surviving in different environmental niches exhibit diverse adaptive metabolic attributes that can help to mitigate the adverse impacts of the extreme environments in which they live. Microbes living in extreme conditions show immense potential to adapt under stressful conditions; therefore, exploitation of plant–microbe interactions should be the most promising approach in the agricultural sector to increase and maintain food productivity in order to sustain food

security (Kumar et al. 2018). Moreover, utilization of beneficial plant–microbe interactions is the most eco-friendly approach to achieve these goals. Application of plant growth–promoting rhizobacteria (PGPRs) as bioinoculants could offer a great potential strategy to minimize deleterious effects of abiotic threats on crops, which cause significant declines in plant growth and yields (Enebe and Babalola 2018). PGPRs could play an important role in management of salinity and drought stresses in plants, as reports have indicated that such beneficial soil microorganisms have a propensity to colonize the root–soil area (rhizosphere) and the endo-rhizosphere of plants to enhance abiotic stress resistance in plants.

There are several strategies through which microbes promote plant growth, such as increases in 1-aminocyclopropane-1-carboxylate (ACC) deaminase; regulation of ethylene levels; and production of the auxin indole-3-acetic acid (IAA), cytokinin, exopolysaccharide (EPS), volatile compounds etc. Further, there are significant increases in osmolyte accumulation and antioxidant enzyme activity, modulation of stress response gene expression levels and changes in root morphology to improve drought tolerance in plants (Khan et al. 2019). Reports have indicated that ACC deaminase–producing PGPRs not only are involved in improving plant growth but also can induce sufficient protection against abiotic stresses (such as drought, salinity, flooding and inorganic and organic contaminants) and biotic stresses (bacterial and fungal pathogens) in plants (Glick 2014). Moreover, it has been reported that production of IAA by a wide variety of soil microorganisms contributes significantly to plant root system development, thereby helping to reduce drought stress (Sharma et al. 2015). Furthermore, to maintain osmotic balance and homeostasis, PGPRs secrete plant growth regulators and enzymes such as IAA and ACC deaminase, among others, which act as signalling molecules in stress conditions, leading to induction of stress response pathways in plants to improve their stress tolerance (Gayathri and Donald 2018).

Recently, Barra et al. (2016) pointed out the importance of rhizocompetent stress-tolerant bacterial strains with variable activity of ACC deaminase and production of IAA for reducing the effects of salinity stress in plants. This indicates that understanding of plant–microbe interactions and their roles in improving stress tolerance under adverse conditions can be a potential tool in agriculture for sustainable production in adverse conditions through optimization of plant–microbe interactions. PGPRs are economically and environmentally beneficial for plant growth promotion. PGPRs alter physico-biochemical and molecular mechanisms in plants, helping them to withstand adverse environmental conditions. Plant–microbe interactions perform a wide range of functions and confer mutual benefits on the plants and microbes. The plants provide the microbes with reduced carbon and other metabolites for growth; in return, the microbes offer certain advantages to the plants. PGPRs have great importance in agricultural systems because they play important roles in enhancing plant growth and yield through effective nutrient acquisition and assimilation. Moreover, PGPRs improve soil texture and secrete important extracellular signalling compounds, hormones, secondary metabolites etc., which further boost plant growth and tolerance of stress. It has been reported that PGPRs are involved in positively modulating plant responses to both biotic and abiotic stresses.

Therefore, they act as biostimulants that can increase crop resilience against adverse conditions, hence offering a potential tool to be utilized to maintain agricultural sustainability by reducing dependency on agrochemicals.

This chapter discusses the effects of PGPRs in the resilience of plants against biotic and abiotic stresses. It also suggests development of suitable bioinoculants for application to different crops, along with other approaches to provide protection from abiotic stresses and tolerance of biotic stresses.

1.2 Rhizobacteria as Beneficial Agents

Microorganisms are an integral component of the biotic system on earth. As an integral part of the biotic component of the rhizosphere, they establish fine interactions with plants, which play vital roles in agricultural systems. As an important natural partner in the rhizosphere, microbes are capable of establishing diverse symbiotic associations with plants. The rhizosphere is the zone surrounding the root system of the plant, which is enriched with a wide variety of nutrients and exudates composed of amino acids, sugars, carbohydrates etc. These support the growth of microbes; therefore, the rhizosphere has a higher density of microorganisms than those of soils in other places. The diverse bacteria that occupy the natural rhizospheric habitat are referred to as rhizobacteria (Schroth and Hancock 1982).

Depending on their interactions with plants and their impacts on plant growth-promoting attributes, rhizobacteria can be categorized into harmful, beneficial and neutral groups (Dobbelaere et al. 2003). Among the diverse groups of free-living bacteria present in the rhizosphere, those groups of rhizobacteria that exhibit plant growth-promoting characteristics are known as plant growth-promoting rhizobacteria (Kloepper et al. 1989). Those that colonize the rhizosphere, live on root surfaces (also known as the rhizoplane) or live inside the roots exhibit growth-promoting potential. It is estimated that only 1–2% of bacteria exhibit plant growth-promoting features, have beneficial effects on plant growth and strengthen plant tolerance against environmental stresses and biotic threats (Antoun and Kloepper 2001).

Among the different genera of bacteria that have been studied, *Bacillus* and *Pseudomonas* spp. have been identified as the most predominant PGPR genera (Podile and Kishore 2007). PGPRs can help plants to resist stresses and maintain plant growth and normal physiological functions. Although there is an abundance of beneficial soil bacteria in the rhizosphere, they have still not been adequately studied and characterized, because there is a dearth of relevant information. To date, this has limited their application as bioinoculant tools in the agricultural sector to mitigate environmental and biotic stresses (Ojuederie et al. 2019). Rhizobacteria of the genera *Pseudomonas* and *Bacillus* are considered the most effective ones in terms of their ability to trigger plant resistance against stresses through induction of systemic resistance and antagonistic effects on pathogens (Table 1.1) (Kloepper et al. 2004; Van Wees et al. 2008; Beneduzi et al. 2012). Exploitation of the roles of

Table 1.1 Plant growth–promoting bacteria (PGPRs) associated with mediation of systemic resistance against pathogens in different crop plants

PGPR strains	Crops	Diseases	Pathogens	References
<i>Pseudomonas fluorescens</i> GRP3	Rice	Sheath blight	<i>Rhizoctonia solani</i>	Pathak et al. (2004)
<i>Pseudomonas fluorescens</i>	Pearl millet (<i>Pennisetum glaucum</i>)	Downy mildew	<i>Sclerospora graminicola</i>	Raj et al. (2003)
<i>Bacillus</i> spp.	Rice	Bacterial leaf blight	<i>Xanthomonas oryzae</i>	Udayashankar et al. (2011)
<i>Pseudomonas</i> sp.	Potato, lettuce	Rhizoctonia diseases	<i>Rhizoctonia solani</i>	Schreiter et al. (2018)
<i>Bacillus pumilus</i> , <i>Paenibacillus costume</i> , <i>Mycobacterium immunogenum</i>	Tomato	Root-knot disease	Nematode (<i>Meloidogyne incognita</i>)	Cetintas et al. (2018)
<i>Pseudomonas putida</i> strain NH-50	Sugar cane	Red rot	<i>Glomerella tucumanensis</i> (Speg.) Arx & E. Müll.	Hassan et al. (2011)

PGPRs as important components in plant–rhizobacteria systems, conferring beneficial effects on agricultural systems, has proved to be an effective strategy in agricultural sustainability and mitigation of biotic and abiotic stresses arising from climate change and other anthropogenic activities. Various types of microbes—*Bacillus* (Kasim et al. 2016), Micrococcaceae HW-2 (Hong et al. 2016), *Pseudomonas*, *Microbacterium*, *Curtobacterium* (Cardinale et al. 2015), *Bradyrhizobium* (Masciarelli et al. 2014), *Pantoea* (Damam et al. 2014), *Variovorax*, *Paenibacillus* (Yolcu et al. 2011) and many others—have shown plant growth–promoting attributes and potential for stress mitigation. Different studies have revealed that soil microorganisms possess the ability to mitigate adverse impacts of abiotic stresses (drought, salinity, extreme temperatures, heavy metal contamination etc.) on plants. Some of these confer tolerance of salinity and drought (*Azospirillum* sp., *Pseudomonas syringae*, *Pseudomonas fluorescens* and *Bacillus* spp.) and nutrient deficiency (*Bacillus polymyxa* and *Pseudomonas alcaligenes*) (Table 1.2) (Chakraborty et al. 2015).

1.3 Plant–Rhizobacteria Interactions and Abiotic Stress Tolerance

Studies have indicated that PGPRs are involved directly or indirectly in increasing crop resilience against various abiotic stresses. In one study, priming of chickpea genotypes with a PGPR consortium culture (*Bacillus subtilis*, *Bacillus thuringiensis* and *Bacillus megaterium*) revealed improved tolerance under drought stress. This

Table 1.2 Plant growth–promoting bacteria (PGPRs) associated with abiotic stress tolerance in different crop plants

Types of stress	PGPR strains	Mechanisms	Crops	References
Drought	<i>Achromobacter piechaudii</i> ARV8	ACC deaminase activity	Tomato	Mayak et al. (2004a)
Drought	<i>Pseudomonas</i> spp.	ACC deaminase activity	Pea (<i>Pisum sativum</i> L.)	Arshad et al. (2008)
Drought	<i>Bacillus</i> spp.	Siderophore production, IAA, phosphate solubilization	<i>Sorghum bicolor</i>	Grover et al. (2014)
Drought	<i>Ochrobactrum pseudogrignonense</i> RJ12, <i>Pseudomonas</i> sp. RJ15, <i>Bacillus subtilis</i> RJ46	ACC deaminase activity	<i>Vigna mungo</i> L., pea (<i>Pisum sativum</i> L.)	Saikia et al. (2018)
Drought, salinity	<i>Burkholderia cepacia</i>	ACC deaminase activity, exopolysaccharide	<i>Capsicum annuum</i>	Maxton et al. (2018)
Drought	<i>Variovorax paradoxus</i> , <i>Pseudomonas</i> spp., <i>Achromobacter</i> spp., <i>Ochrobactrum anthropi</i>	ACC deaminase activity	Wheat (<i>Triticum aestivum</i> L.)	Chandra et al. (2019)
Drought	<i>Pseudomonas putida</i> , <i>Bacillus amyloliquefaciens</i>	ACC deaminase activity	Chickpea (<i>Cicer arietinum</i> L.)	Kumar et al. (2016)
Salinity	<i>Bacillus</i> spp.	IAA, ACC deaminase activities	Rice	Mishra et al. (2017)
Salinity	<i>Enterobacter</i> spp.	ACC deaminase activity	Rice	Sarkar et al. (2018)
Salinity	<i>Mesorhizobium</i> spp.	ACC deaminase activity	Chickpea (<i>Cicer arietinum</i> L.)	Chaudhary and Sindhu (2017)
Salinity	<i>Streptomyces</i> spp.	Auxin activity	Wheat (<i>Triticum aestivum</i>)	Sadeghi et al. (2012)
Salinity	<i>Klebsiella</i> sp. MBE02	Auxin activity	<i>Arachis hypogea</i>	Sharma et al. (2016)

ACC 1-aminocyclopropane-1-carboxylate, IAA indole-3-acetic acid

improved tolerance correlated with increased relative water content (RWC) and enhanced accumulation of various osmolytes (succinate, leucine, disaccharide, saccharic acid and glyceric acid), along with other metabolites, in chickpea genotypes. PGPRs have the ability to induce plant tolerance under abiotic stress by regulation of various physiological and metabolic pathways (Khan et al. 2019).

Several types of bacteria—such as *Azospirillum*, *Klebsiella*, *Burkholderia*, *Bacillus* and *Pseudomonas*—have been identified as PGPRs in maize cropping systems. The term ‘induced systemic tolerance’ (IST) refers to increasing tolerance in plants through modulation of physical and chemical processes triggered by microorganisms when the plants are exposed to a stressful situation. One study revealed that PGPRs have immense ability to increase tolerance of salinity stress by approximately 50% in maize and wheat; therefore, application of PGPRs leads to significantly enhanced crop resilience under salinity stress and improved crop productivity in wheat (Orhan 2016). With the frequent incidence of abiotic stress, there is always a major concern to identify and develop strategies that can be used to mitigate the deleterious impacts of abiotic stress on crop growth and yields. Various research activities—involving genetic engineering, plant breeding, resource management practices etc.—are under way to develop stress-tolerant plant varieties, but many of these technologies are time consuming and costly. However, the results of several studies have now supported the potential role of microorganisms in helping plants deal with drought and salinity stress through improved tolerance (Vurukonda et al. 2016).

Plant growth-promoting bacteria (PGPBs), which are bioeffector microbes, can offer several benefits to the agricultural sector with appropriate application. PGPBs can induce plant growth and ameliorate plant resilience against biotic and abiotic stresses (Ventorino et al. 2016). Therefore, exploration of the plant growth-promoting activities of several bacterial strains isolated from different extreme environments may provide important information to broaden the range of applications of PGPRs as a potential tool in agricultural sustainability.

There are various reports available on beneficial soil microorganisms showing PGPR attributes. They note that soil microorganisms in areas where the conditions are extreme show better adaptations to survive under those situations. Such microbes could therefore be of great help if used in agriculture to increase tolerance and crop productivity. Moreover, it is now accepted that beneficial soil microorganisms possess important attributes that can increase crop tolerance and improve plant growth and productivity under abiotic and biotic stresses in several ways such as mobilization of nutrients, improvement of soil texture and health, secretion of plant growth regulators, disease suppression etc. (Verma et al. 2016). PGPRs isolated from places with less rainfall are better able to survive and extend protection to plants by increasing their tolerance of desiccation. Mayak et al. (2004a) noted that PGPRs isolated from areas with low rainfall are more effective in this regard than other similar bacteria isolated from sites with sufficient availability of water. For instance, the bacterial strain *Achromobacter piechaudii* ARV8, isolated from rhizospheric soil in a dry region, exhibited ACC deaminase activity that induced significant drought tolerance in tomato. Other researchers have also demonstrated protective effects of ACC deaminase production by PGPRs on different plants against loss of biomass from drought stress (Belimov et al. 2009; Shakir et al. 2012; Penrose and Glick 2003). The same mechanism is equally effective against salinity stress, which otherwise causes plants to suffer more inhibition of growth and development (Mayak et al. 2004b).

PGPRs produce a variety of primary or low molecular weight secondary metabolites—proline, glycine betaine, sugars, polyamines, amides and other enzymes, EPS etc.—that help plants to enhance their abiotic stress tolerance under adverse conditions (Jha et al. 2011; Kasotia et al. 2016; Kurz et al. 2010; Singh and Jha 2016). Production of various secondary metabolites by salinity-tolerant rhizobacteria has shown the potential capability to induce salinity stress tolerance in plants by improving their physiological conditions. Application of such rhizobacteria therefore has the potential for mitigation of salinity stress to improve crop productivity (Mishra et al. 2018).

PGPRs that express ACC deaminase activity decrease plant ethylene levels, as this enzyme breaks down the ethylene precursor ACC to α -ketobutyrate and ammonium, leading to decreased ethylene concentrations in stressed plants and improved plant tolerance of stress. Notably, ACC deaminase-producing rhizobacteria confer induced tolerance in plants against a wide range of different biotic and abiotic stresses through effective plant–microbe interactions (Glick et al. 2007). Among various different crop management practices used in the agricultural sector, application of PGPRs via different methods (such as seed priming or application to the soil) is important to achieve the desired effects in protecting plants against stress. The underlying mechanism of PGPR involvement in reduction of plant ethylene levels is metabolization of the ethylene precursor at the root–soil interface under stress conditions, thereby improving crop yields (Belimov et al. 2009). The stress-induced increase in plant ethylene levels varies depending on the genotype and the magnitude of the stress. Therefore, it is suggested that opportunities for better management and application of PGPRs in agricultural systems should be explored to improve water use and carbon gains in field crops.

A recent study on drought stress tolerance in two important crops—mung bean (*Vigna mungo* L.) and pea (*Pisum sativum* L.)—found that a consortium of rhizobacteria strains (*Ochrobactrum pseudogrignonense* RJ12, *Pseudomonas* sp. RJ15 and *Bacillus subtilis* RJ46) had the ability to produce ACC deaminase. The results indicated improved tolerance in these crops, due to ACC deaminase activity leading to decreased ACC accumulation and regulation of ethylene levels (Saikia et al. 2018). Grover et al. (2014) conducted a study on sorghum and revealed that inoculation with different strains of *Bacillus* spp. imparted improved tolerance of moisture stress conditions, improving seedling growth and physiological attributes. This improved tolerance was attributed to phosphate solubilization and production of IAA and siderophores. Further, improved drought and salinity stress tolerance were observed in *Capsicum annuum* when it was inoculated with *Burkholderia cepacia*. It was reported that ACC deaminase activity of PGPRs promoted growth and development in conditions of drought and salinity stress (Maxton et al. 2018). Chandra et al. (2019) studied the impact of PGPRs on wheat (*Triticum aestivum* L.) under drought stress. Inoculation of the wheat with *Variovorax paradoxus* RAA3, *Pseudomonas* spp., *Achromobacter* spp. and *Ochrobactrum anthropi* improved seedling growth, which correlated with increased activity of ACC deaminase, siderophore production and phosphate solubilization properties of PGPRs under drought stress (Chandra et al. 2019). Mishra et al. (2017)

conducted a study on rice inoculated with different rhizobacteria (*Bacillus* spp.) collected from various agroclimatic zones under salinity stress. The results indicated that production of ACC deaminase and IAA by these rhizobacteria improved seedling growth under salinity stress.

Abiotic stresses—mainly drought, salinity and extreme temperatures—affect plant growth and limit crop productivity significantly. Plants have an inherent ability to cope with adverse conditions but only to a limited extent. Several genetic engineering tools and breeding methods are available for crop improvement to develop tolerance of abiotic and biotic stresses in plants. The role of soil microorganisms cannot be ignored. Our present understanding of beneficial soil microorganisms in the rhizosphere and their immense potential for improving plant tolerance of both biotic and abiotic stresses offers an alternate eco-friendly approach to develop crop resilience under stress.

Plant–rhizobacterium interactions involve modulation of various physiological, biochemical and molecular pathways under stressful conditions to boost tolerance. We still do not fully understand the exact mechanisms through which PGPRs impart their beneficial effects on plants and modulate different signalling networks to improve tolerance under abiotic stress. It has been suggested that plant–rhizobacteria interactions facilitate increase nutrient uptake, maintain plant water relations and enhance photosynthesis and source–sink relationships to boost plant growth and yields. PGPRs modulate several physiological, cellular, biochemical and molecular processes to improve plant tolerance under abiotic stress (Gayathri and Donald 2018). Diverse groups of microbes have been identified as having the ability to catabolize plant exudates, leading to protection of the plants from drought and salinity stress. PGPRs produce a wide variety of substances—ACC deaminase (Saleem et al. 2015), siderophores (Stajkovic-Srbincovic et al. 2014), plant growth regulators, salicylic acid (Ekinici et al. 2014), the phytohormone IAA (Gujral et al. 2013), phosphate-solubilizing enzymes (Kumari and Khanna 2016) and microbiocidal and biostatic enzymes (Moustaine et al. 2017)—which boost important biochemical and physiological processes involved in plant defence against stresses.

Plant–rhizobacteria interaction increase plant defence by modulating several cellular processes, improving photosynthesis, nutrient uptake and source–sink relationships and thereby improving plant growth. PGPRs exhibit the ability to modulate several factors—such as phytohormones status, protein function, gene expression and metabolite synthesis in plants—improving their defence responses. Enhanced antioxidant activity, accumulation of osmolytes, salt compartmentalization etc. reduce osmotic stress and the effects of ion toxicity in response to salinity stress and drought stress. Moreover, extracellular signalling molecules trigger stress-responsive pathways in plants to help them cope better with adverse conditions (Gayathri and Donald 2018).

1.4 Plant–Rhizobacteria Interaction and Biotic Stress Tolerance

Phytopathogens are the principal causes of biotic stress in crops, leading to substantial decreases in crop yields and crop losses. PGPRs can help plants to resist phytopathogens and biotic stresses by adopting appropriate strategies against such threats, including antagonism and triggering of systemic resistance. The presence of PGPRs in the soil has a profound effect on the soil characteristics. They secrete several different groups of compounds, thereby increasing the quality of the soil for better cultivation (Gouda et al. 2017). It is also important to note that appropriate application of PGPRs in crops also depends greatly on their compatibility with the soil type and with other indigenous microbes in the soil (Singh et al. 2016).

PGPRs possess several plant growth–promoting attributes and secrete groups of compounds that confer plant tolerance of both abiotic and biotic stresses. Different species of PGPRs (such as *Bacillus*) that are present in agricultural fields can promote plant growth and development either by increasing the availability of nutrients or by triggering plant defences against plant pathogens, infections, insect attacks etc. (Kumar et al. 2012; Egamberdieva and Lugtenberg 2014). A study conducted in tomato revealed that methyl jasmonate (MeJA) and the ethylene precursor ACC can boost resistance against *Pseudomonas syringae* pv. *tomato* (Pieterse et al. 1998, 2000). In another study on increased resistance against bacterial canker disease, which is caused by *Clavibacter michiganensis* subsp. *michiganensis* (*Cmm*), it was suggested that treatment of tomato (*Solanum lycopersicon* L.) plants with *Pseudomonas* sp. 23S triggered induced systemic resistance (ISR) in the plants and reduced the severity and progression of the disease. It was further suggested that it was salicylic acid that mediated induced systemic resistance in the plants (Takishita et al. 2018). Application of salicylic acid resulted in better tolerance of *Rhizoctonia solani* in cowpea by enhancing phenylalanine ammonia lyase (PAL) activity (Chandra et al. 2007).

Use of PGPRs as biocontrol agents offers an eco-friendly option for control of plant diseases. Presently, several PGPR species of different genera are used as biocontrol agents—*Agrobacterium*, *Azotobacter*, *Azospirillum*, *Bacillus*, *Delftia*, *Burkholderia*, *Rhizobium*, *Paenibacillus*, *Pantoea*, *Pseudomonas* and *Serratia*—to combat plant pathogens and prevent disease progression (Glick 2012). Application of PGPR strains belonging to the important genera *Bacillus* and *Pseudomonas* as biocontrol agents in cannabis plants achieved improvements in yield and growth under stress and provided better tolerance against powdery mildew, which is the most common pathogen affecting cannabis yields (Lyu et al. 2019). The competence of *Pseudomonas* sp. RU47 as a biocontrol agent in the rhizospheres of two important crops—potato (*Solanum tuberosum* L.) and lettuce (*Lactuca sativa* L.)—was studied by Schreiter et al. (2018), who found that its application as a bioinoculant was an effective strategy to control the effects of disease caused by the plant pathogen *Rhizoctonia solani*.

In recent years, biocontrol of plant-parasitic nematodes through antagonism by PGPR application has attracted considerable attention, and studies have been conducted to assess the potential of PGPRs as biocontrol agents to protect plants from disease-causing phytonematodes (Sidhu 2018). Application of PGPRs (*Bacillus pumilus*, *Paenibacillus costume* and *Mycobacterium immunogenum*) was found to be an effective biocontrol strategy against the nematode *Meloidogyne incognita*, which causes root rot disease in tomato (Cetintas et al. 2018). Similarly, biocontrol effects of different rhizobacterial strains (*R. leguminosarum* and *P. fluorescens*) were observed in different legume crop rhizospheres, leading to decreased pathogenesis due to root-knot nematodes (*Meloidogyne javanica*) and improved seedling growth (Tabatabaei and Saedizadeh 2017). Application of PGPRs in rice resulted in effective suppression of the phytopathogen *Xanthomonas oryzae* pv. *oryzae* (which is responsible for bacterial blight disease in rice) and also achieved effective resistance to blister blight disease (caused by the phytopathogen *Exobasidium vexans* Massee) in tea (Suryadi et al. 2019). Inoculation with the PGPR *Pseudomonas putida* strain NH-50, which has the ability to produce pyoluteorin, was found to significantly reduce red rot disease in sugar cane by inhibiting growth of *Glomerella tucumanensis* (Speg.) Arx & E. Müll. (Hassan et al. 2011).

1.4.1 Mechanisms of Rhizobacteria-Mediated Phytopathogen Tolerance in Plants

PGPRs are highly diverse, which can also help induce plant resistance against several types of biotic stress caused by pathogen attacks. Several studies have revealed that PGPRs induce biotic stress tolerance in plants either through local antagonism to soilborne pathogens or through induction of systemic resistance against several pathogens. Nonpathogenic rhizobacteria can interact with plants and stimulate substantial increases in plant capabilities for defence against pathogens and plant diseases. The reduction in disease is associated with decreased pathogen growth and reduced colonization of plant tissue, reflecting the ability of the plants to resist the pathogens. This is the mechanism of induced systemic resistance in plants (Van Loon et al. 1998).

It has been reported that PGPRs act as biocontrol agents by producing various compounds—antibiotics, siderophores etc.—that can control pathogen progression and sustain plant growth. Rhizobacterium-mediated induced systemic resistance in plants and pathogen-induced systemic acquired resistance (SAR) induced by bacteria in plants together induce greater resistance to plant pathogens and disease (Van Loon et al. 1998). Studies have revealed that signalling molecules such as salicylic acid, secreted by rhizobacteria, trigger pathogen resistance in plants through salicylic acid-mediated systemic acquired resistance in the plants, which is induced by pathogen attacks and is followed by activation of pathogenesis-related (PR) proteins. Moreover, secretion of other signalling molecules—such as jasmonic

acid, ethylene and lipopolysaccharides—leads to triggering of induced systemic resistance in plants. Microbial antagonism is one of the mechanisms through which rhizobacteria reduce the impact of pathogens in plants and improve plant tolerance of biotic stress (Beneduzi et al. 2012; Spoel and Dong 2012; Van Wees et al. 2008). Siderophores, bacteriocins and antibiotics are some of the important compounds produced and released by PGPRs, and they are very effective in reducing disease and limiting progression of pathogens in plants through antagonistic activity (Maksimov et al. 2011). Some of the important antagonistic activities that are likely to be dominant in the rhizosphere include synthesis and secretion of hydrolytic enzymes—such as chitinases, glucanases, proteases and lipases—that restrict the activities of fungal pathogens (Maksimov et al. 2011). Regulation of ACC deaminase activity, control of ethylene levels in plant under biotic stress (Kamilova et al. 2005), siderophore production (Van Loon 2007) and competition for suitable space on root surfaces for colonization and nutrient acquisition are some of the strategies exhibited by PGPRs that help induce plant tolerance of pathogen infections.

1.5 Conclusion

The current reality in the agricultural sector is that climate change and frequent occurrences of biotic and abiotic stresses lead to significant limitations in crop productivity. This has prompted research into development of methods to induce the intrinsic defences of plants against such stresses in order to maintain agricultural sustainability. To date, the concept of plant–microbe interactions and the roles of PGPRs have been underexplored, but there is huge potential for exploitation of plant–microbe interactions as potential tools in abiotic stress tolerance and as biocontrol agents for defence against biotic stresses. Commercial development of single rhizobacterial strains or combinations of different rhizobacterial strains as effective biocontrol agents could be exploited for cost-effective, low-input, eco-friendly and sustainable plant management to reduce dependence on agrochemicals in agricultural systems. Moreover, application of PGPRs offers a long-term eco-friendly option to develop both intrinsic and extrinsic abilities of plants to resist biotic and abiotic stressful conditions and to sustain crop growth and yields.

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