

Microorganisms for Sustainability 12

Series Editor: Naveen Kumar Arora

R. Z. Sayyed

Naveen Kumar Arora

M. S. Reddy *Editors*

Plant Growth Promoting Rhizobacteria for Sustainable Stress Management

Volume 1: Rhizobacteria in Abiotic
Stress Management



Springer

Microorganisms for Sustainability

Volume 12

Series editor

Naveen Kumar Arora, Environmental Microbiology, School for Environmental Science, Babasaheb Bhimrao Ambedkar University, Lucknow, Uttar Pradesh, India

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Stress Management

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Foreword



National Academy of Agricultural Sciences



Achieving sustainable agricultural production while keeping the environmental quality, agroecosystem functions, and biodiversity is a real challenge in the present agricultural scenario. The traditional use of chemical inputs (fertilizers, pesticides, nutrients, etc.) poses serious threats to crop productivity, soil fertility, and the nutritional value of farm produce. Global concern over the demerits of chemicals in agriculture has diverted the attention of researchers toward sustainable agriculture by utilizing the potential of plant growth-promoting rhizobacteria (PGPR). Therefore, management of pests and diseases, agroecosystem well-being, and health issues for humans and animals has become the need of the hour. The use of PGPR as biofertilizers, plant growth promoters, biopesticides, and soil and plant health managers has gained considerable attention among researchers, agriculturists, farmers, policymakers, and consumers.

The application of PGPR as a bioinoculant can help in meeting the expected demand of global agricultural productivity to feed the world's booming population, which is projected to reach around 9 billion by 2050. However, to be a useful and

effective bioinoculant, PGPR strain should possess high rhizosphere competence, usefulness to soil rhizobacteria, broad-spectrum activity and tolerance to various biotic and abiotic stresses. PGPR-mediated plant growth promotion and biocontrol is now gaining worldwide importance and acceptance as eco-friendly and effective bioinoculants for sustainable agriculture. However, the performance of PGPR is subject to various abiotic factors such as salinity, temperature (high/low), drought, metal ions, and presence of various toxic compounds. Only those PGPR that establish themselves and can manage such abiotic stress can perform better as plant growth-promoting and biocontrol agents.

This book, which has 17 chapters encompassing the influence of various abiotic factors on the performance of PGPR and written by different experts from India and abroad, is to highlight salient features on the application of PGPR in agricultural crop plants to lend a hand to scientists working in this field. ***PGPR in abiotic stress management*** is a timely effort for sustainable agriculture. I compliment the authors and hope the teachers and researchers working in this area will make use of this publication.



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Preface

The future of agriculture greatly depends on our ability to enhance crop productivity without sacrificing long-term production potential. Agriculture primarily depends on the use of natural resources such as land, soil, water, and nutrients. As demand for food increases and climate change and natural ecosystem damage imposes new constraints, sustainable agriculture has an important role to play in safeguarding natural resources, reducing greenhouse gas emissions, halting biodiversity loss, and caring for valued agricultural practices. Agricultural productivity rests on the foundation of microbial diversity in the soil. The application of microorganisms, such as the diverse bacterial species of plant growth-promoting rhizobacteria (PGPR), represents an ecologically and economically sustainable strategy for agriculture. PGPR are associated with plant roots and augment plant growth and disease management, elicit “induced systemic resistance” to salt and drought, and increase nutrient uptake from soils, thus reducing the need for fertilizers and preventing the accumulation of [nitrates in soils](#). Increased incidences of abiotic and biotic stresses impacting agricultural productivity in principal crops are being witnessed all over the world. Extreme events like prolonged droughts, intense rains and flooding, heat waves, and frost damages are likely to further increase in the future due to climate change. Enhancement of plant drought stress tolerance by PGPR has been increasingly documented in the literature. However, most studies to date have focused on PGPR-plant root interactions, but very little is known about PGPR’s role in mediating physiochemical and hydrological changes in the rhizospheric soil that may impact plant drought stress tolerance. A reduction in fertilizer use would lessen the effects of water contamination from fertilizer runoff and lead to savings for farmers.

There is a need to develop simple and low-cost biological methods for the management of abiotic stress, which can be used on short-term basis. PGPR could play a significant role in this respect if we can exploit their unique properties of tolerance to extremities, their ubiquity and genetic diversity, and their interaction with crop plants and develop methods for their successful deployment in agriculture production.

With the advent of climate change, global agriculture faces a multitude of challenges. The most prominent among these are abiotic stresses imposed by increased incidences of drought, extremes of temperature, and unseasonal flooding. Such atmospheric threats, coupled with edaphic stresses, pose severe challenges to food

production. While several agronomic and plant breeding strategies have been proposed to overcome these phenomena, the utilization of PGPR is receiving increased attention globally.

Achieving sustainable agricultural production while keeping the environmental quality, agroecosystem function, and biodiversity is a real challenge in the current agricultural practices. The traditional use of chemical fertilizers and pesticides poses serious threats to crop productivity, soil fertility, and the nutritional value of farm produce. Global concern over the demerits of chemicals in agriculture has diverted the attention of researchers toward sustainable agriculture by utilizing PGPR. Therefore, management of pests and diseases, agroecosystem well-being, and health issues for humans and animals has become the need of the hour. The use of PGPR as biofertilizers, plant growth promoters, biopesticides, and soil and plant health managers has gained considerable attention among researchers, agriculturists, farmers, policymakers, and consumers.

The application of PGPR as biostimulants can help in meeting the expected demand of global agricultural productivity to feed the world's booming population, which is predicted to reach around 9 billion by 2050. However, to be a useful and effective bioinoculant, PGPR strains should possess high rhizosphere competence, safety to the environment, plant growth promotion and biocontrol potential, compatibility with agronomic practices with broad-spectrum activity, and tolerant to various biotic and abiotic stresses. In view of this, the need for a better PGPR to complement the increasing agro-productivity as one of the crucial drivers of the economy has been highlighted.

PGPR-mediated plant growth promotion and biocontrol is now gaining worldwide importance and acceptance as eco-friendly and effective bioinoculants for sustainable agriculture. However, the performance of PGPR is subject to various abiotic factors such as salinity, temperature (high/low), drought, metal ions, and presence of various toxic compounds. Only those PGPR that establish themselves and can manage such abiotic stress can perform better as plant growth-promoting and biocontrol agents.

The prime aim and objective of this book is to highlight salient features on the application of PGPR in agricultural crop plants to lend a hand to scientists throughout the world working in this field. PGPR in abiotic stress management is a timely effort for sustainable agriculture. These also provide excellent tools for understanding the stress tolerance, adaptation, and response mechanisms that can be subsequently engineered into crop plants to cope with climate change-induced stresses.

This book is composed of 17 chapters encompassing the influence of various abiotic factors on the performance of PGPR to comprehend the information that has been generated on the abiotic stress-alleviating mechanisms of PGPR and their abiotic stress alleviation potential. Agricultural crops grown on saline soils suffer on an account of high osmotic stress, nutritional disorders and toxicities, poor soil physical conditions, and reduced crop productivity. The various chapters in this book focus on the enhancement of productivity under stressed conditions and increased resistance of plants against salinity stress by the application of PGPR.

It has been an immense pleasure to edit this book, with continued cooperation of the authors. We wish to thank Dr. Mamta Kapila, Ms. Raman Shukla, and Mr. Sivachandran Ramanan at Springer, India, for their generous cooperation in completion of this book.

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Contents

1	The Role of Plant Growth-Promoting Rhizobacteria to Modulate Proline Biosynthesis in Plants for Salt Stress Alleviation	1
	Shamim Ahmed, Aritra Roy Choudhury, Poulami Chatterjee, Sandipan Samaddar, Kiyoon Kim, Sunyoung Jeon, and Tongmin Sa	
2	Plant Growth-Promoting Rhizobacteria and Salinity Stress: A Journey into the Soil	21
	Bahman Fazeli-Nasab and R. Z. Sayyed	
3	Dark Septate Endophytes and Their Role in Enhancing Plant Resistance to Abiotic and Biotic Stresses	35
	Iman Hidayat	
4	Rhizobacteria and Abiotic Stress Management	65
	Naeem Khan, Asadullah, and Asghari Bano	
5	Plant Growth-Promoting Rhizobacteria: Benign and Useful Substitute for Mitigation of Biotic and Abiotic Stresses	81
	Jyoti Singh, Prachi Singh, Shatrupa Ray, Rahul Singh Rajput, and Harikesh Bahadur Singh	
6	Rhizospheric Microflora: A Natural Alleviator of Drought Stress in Agricultural Crops	103
	J. Patel Priyanka, R. Trivedi Goral, K. Shah Rupal, and Meenu Saraf	
7	Quorum Sensing Molecules of Rhizobacteria: A Trigger for Developing Systemic Resistance in Plants	117
	Mahejibin Khan, Prachi Bhargava, and Reeta Goel	
8	Zinc-Solubilizing Bacteria: A Boon for Sustainable Agriculture	139
	Ashok Kumar, Savita Dewangan, Pramod Lawate, Indra Bahadur, and Srishti Prajapati	
9	Rhizobacteria as Bioprotectants Against Stress Conditions	157
	F. Pereira	

10	Rhizobacteria for Reducing Heavy Metal Stress in Plant and Soil	179
	Biplab Dash, Ravindra Soni, and Reeta Goel	
11	Pesticide Residues in the Soil Cause Cross-Resistance Among Soil Bacteria	205
	Rangasamy Kirubakaran, Athiappan Murugan, Newsheen Shameem, and Javid A. Parray	
12	Psychrotrophic Microbes: Biodiversity, Mechanisms of Adaptation, and Biotechnological Implications in Alleviation of Cold Stress in Plants	219
	Ajar Nath Yadav, Divjot Kour, Sushma Sharma, Shashwati Ghosh Sachan, Bhanumati Singh, Vinay Singh Chauhan, R. Z. Sayyed, Rajeev Kaushik, and Anil Kumar Saxena	
13	Drought-Tolerant Phosphorus-Solubilizing Microbes: Biodiversity and Biotechnological Applications for Alleviation of Drought Stress in Plants	255
	Divjot Kour, Kusam Lata Rana, Ajar Nath Yadav, Neelam Yadav, Vinod Kumar, Amit Kumar, R. Z. Sayyed, Abd El-Latif Hesham, Harcharan Singh Dhaliwal, and Anil Kumar Saxena	
14	Role of PGPR for Alleviating Aluminum Toxicity in Acidic Soil	309
	Jintu Dutta and Utpal Bora	
15	Rhizobacteria: Legendary Soil Guards in Abiotic Stress Management	327
	Afreen Khan, R. Z. Sayyed, and Sonia Seifi	
16	Rhizobacteria–Plant Interaction, Alleviation of Abiotic Stresses	345
	R. K. Singh, Prahlad Masurkar, Sumit Kumar Pandey, and Suman Kumar	
17	Role of Rhizobacteria in Drought Tolerance	355
	Meghmala Waghmode, Aparna Gunjal, Neha Patil, and Neelu Nawani	

About the Series Editor



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The Role of Plant Growth-Promoting Rhizobacteria to Modulate Proline Biosynthesis in Plants for Salt Stress Alleviation

1

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Abstract

Soil salinization causes serious problem to environmental resources and human health in many countries. Around 1.5 billion hectares of cultivated lands are present in the world. It is estimated that almost 5% of the cultivated land (77 million) and 6% of total surface land is affected by salinity. Agricultural crops and their productivity are severely affected by salt stress. Many physiological mechanisms within the plants are regulated when exposed to salt stress. The salinity tolerance measurement has a great demand to assess the regulatory variations, growth, and survival parameters. Microorganisms that colonize the roots could play a significant role in this aspect. Rhizobacteria which possess properties such as salt tolerance, nutrient uptake ability, synthesis of compatible solutes, production of plant growth-promoting hormones, biocontrol potential, and their interaction with crop plants is known as plant growth-promoting rhizobacteria (PGPRs). Proline is one of the essential compatible solute for both plant and bacteria to respond against osmotic imbalance and ionic toxicity. Proline biosynthesis occurs in cytosol and mitochondria of a cell and modulates their functions in various cellular physiological pathways. It can also influence the proliferation and apoptosis of cell and regulate specific gene expression to alleviate salt stress. Rhizobacteria having plant growth promoting characteristics can be used as a suitable bio-inoculant to promote growth and productivity through different mechanisms in addition to the accumulation of proline as osmoregulators.

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Keywords

Salinity · Microbial inoculants · Osmoregulators · Proline · Ornithine-delta-aminotransferase (OAT)

1.1 Introduction

The recent adversity of salinity is one of the ferine factors for crop production around the globe. In addition to global climate change, salt stress causes serious reduction of crop production, which accounts up to 20–50% of yield loss (Shrivastava and Kumar 2015). Intensive breeding of tolerant varieties, farm improvement, and quality resource management can help to overcome salinity stress. Nowadays, these technologies are quite intensive, tardy, and prolux (Grover et al. 2011) being less eco-friendly to solve that matter. The production of agrochemicals is energetically expensive and dependent on fossil fuels that are nonrenewable resources, which makes it no longer sustainable.

In agricultural point of view, it is essential to develop an easily applicable technique for the farmers. Cost-effective biological methods for salinity stress management within a short-term basis might be the appropriate alternative. To enhance the availability of essential plant nutrients and their mobilization (especially phosphorus) for crop production, biological inoculation (living organisms containing strains of specific bacteria, fungi, or algae) has high demand. The recent concern is to improve the existing bio-inoculation techniques for the development of next-generation biofertilizer.

1.2 Salt Stress

Researchers have been studying the various responses of plants to abiotic stress for developing techniques which can ramify the stress effect. Salinity stress affects the growth and survival of the plant. Due to increase in poor irrigation facilities and soil salinization, the soil becomes saline ($EC > 4 \text{ dSm}^{-1}$) or sodic ($EC < 4 \text{ dSm}^{-1}$). Sodium absorption ratio in saline soil is less than 13 ($\text{pH} < 8.5$) and in sodic soil is more than 13 ($\text{pH} < 8.5$) (Selvakumar et al. 2014). The plant's exposure to salinity results in negative impact on various physiological and biochemical pathways which affects the growth and survivability. Hence, it is important to measure the degree of salinity of a particular cultivable land (Albaladejo et al. 2017).

1.2.1 Adverse Effects of Salt Stress in Plant

Salt stress negatively affects the plants in three distinct ways, viz., osmotic imbalance, ionic toxicity, and reduction in nutrient uptake (Selvakumar et al. 2014). Osmotic imbalance due to high salinity condition makes plants harder to take up

water by root from that soil. The immediate effect of salt exposure results in loss of turgidity, cell dehydration and ultimately cell death. On the other hand, adverse effects of salinity on plant growth may also result to impairment of the supply of photosynthetic assimilates or hormones to the growing tissues (Ashraf 2004). Under salt stress, ionic toxicity occurs through the replacement of K^+ by Na^+ which induces conformational changes in proteins (Maathuis and Amtmann 1999). For several enzymes, K^+ acts as a cofactor and cannot be substituted by Na^+ (Pessarakli 2016). Na^+ and Cl^- ions are mostly uptaken by the cell vacuoles and organic solutes which are compatible with metabolic activity even at high concentrations are accumulated in the cytosol (Baetz et al. 2016). These compatible solutes helps to balance the osmotic pressure of the ions in the vacuoles (Flowers and Colmer 2008). Many current studies reported that salt stress not only adversely affects the growth and development of plant but also hinders their seed germination, seedling growth, and enzyme activity (Seckin et al. 2009). High salinity has been reported to induce ROS formation and accumulation in the plant cell (Chawla et al. 2013). Overall, salinity has adverse effect on plethora of biochemical and physiological activities of plants (Tabur and Demir 2010).

1.2.2 Adverse Effects of Salt Stress in Bacteria

Microbial diversity, composition, and their abundance are also affected by soil salinity (Borneman et al. 1996). The bacterial and actinobacterial abundance was observed to be drastically reduced when salinity level increased about 5% (Omar et al. 1994). NifH expression and nitrogenase activity level were inhibited by nitrogen fixation in *Azospirillum* sp. under salt-containing rhizospheric soil (Tripathi et al. 2002). Root exudation and decomposition of organic matter by microorganisms were also affected by increasing salinity of the soil (Ondrasek et al. 2010).

1.3 Potential Use of Bio-inoculant for Salt Stress Alleviation

Microorganisms, which can colonize the roots, might play a significant role for the alleviation of salt stress. The exploitation of their unique properties for salt tolerance can be considered for development of effective bio-inoculant for plant growth promotion and salt stress alleviation. The general properties for the development of a potential bio-inoculant should include salt tolerance, production of plant growth-promoting hormones, genetic diversity, synthesis of compatible solutes, and their positive interaction with crop plants. An increasing number of farmers are choosing biofertilizers (Chatzipavlidis et al. 2013) since they are harmless for the soil and can help reduce the negative impact of global climate change. Biofertilizers can supplement nutrients to plants, particularly micronutrients, and contribute to increasing soil organic matter, in addition to being active in small numbers and able to self-multiply (Berg 2009).

1.4 Microorganisms for the Alleviation of Salt Stress

Beneficial soil microorganisms can promote growth and increase productivity through various mechanisms such as nutrient mobilization, hormone secretion, and disease suppression (Table 1.1). It is also becoming clear that their effects will be more far-reaching. Diverse halotolerant bacterial groups mostly belong to four phyla, δ -Proteobacteria, α -Proteobacteria, Bacteroidetes, and Verrucomicrobia, which are involved in alleviating salt stress. The genera *Microbulbifer* (*Alteromonadales*), *Pelagibius* (*Rhodospirillales*), *Halomonas* (*Oceanospirillales*), *Marinoscillum* (*Sphingobacteriales*), *Fulvivirga* (*Flexibacteraceae*), *Haloferula* (*Verrucomicrobiales*), *Pelagicoccus* (*Puniceicoccales*), and *Marinobacter* (*Alteromonadales*) were exclusively enriched in the rhizospheric soil, with the exception that *Marinobacter* was more abundant in the root endosphere than in the bulk or rhizosphere soil (Yuan et al. 2016) (Table 1.1).

1.5 The Role of Plant Growth-Promoting Rhizobacteria (PGPRs) for the Alleviation of Salt Stress

Plant growth-promoting rhizobacteria (PGPRs) could enhance crop yield under salinity conditions through nutrient uptake and plant growth-promoting characteristics (Fig. 1.1). PGPR as rhizo-remediators could prevent the deleterious effects of xenobiotics and act as biocontrol agents by producing antibiotics (Bouizgarne 2013). They can trigger induced local or systemic resistance for biotic and abiotic stress tolerance (Jacobsen 1997; Somers et al. 2004; Aseri et al. 2008; Glick et al. 2007; Van Loon 2007). Instead of using chemical fertilizer, their application as bio-inoculants for agricultural purposes would be a suitable alternative (Bloemberg and Lugtenberg 2001; Vessey 2003). The dominant α -Proteobacteria and γ -Proteobacteria communities in bulk soil and root endosphere tend to be phylogenetically clustered and contribute to salt stress acclimatization, nutrient solubilization, and competitive root colonization (Yuan et al. 2016). The effective existence of bacteria in the saline environment due to excessive accumulation of secondary metabolites may result in better root colonization and plant growth. Accumulation of small organic molecules also known as compatible solutes in response to salinity is reported in all living groups to a variable extent (Saharan and Nehra 2011).

1.6 Importance of Compatible Solute to Mitigate Salt Stress After Inoculation of PGPRs

Compatible solutes are usually nontoxic, low molecular weight organic compounds and easily soluble at high cellular concentrations (Hayat et al. 2012). At low concentrations, these solutes presumably have another role, perhaps in stabilizing the tertiary structure of proteins, and function as osmoprotectants. These solutes provide protection to plants from stress by contributing to cellular osmotic adjustment,

Table 1.1 List of bacterial endophytes with the possible mechanism of alleviating salt stress

Pathway	Bacteria	Plants	References
Cytokinin signaling and stimulation of shoot biomass	<i>Bacillus subtilis</i>	<i>Lactuca sativa</i>	Arkhipova et al. (2007)
Expression of salt stress-related <i>RAB18</i> plant gene	Root-associated plant growth-promoting rhizobacteria (PGPRs)	<i>Oryza sativa</i>	Jha et al. (2014)
Tissue-specific regulation of sodium transporter HKT1	<i>Bacillus subtilis</i> GB03	<i>Arabidopsis thaliana</i>	Zhang et al. (2008)
SA-dependent pathway	<i>Pseudomonas syringae</i> DC3000, <i>Bacillus</i> sp. strain L81, <i>Arthrobacter oxidans</i>	<i>Arabidopsis thaliana</i>	Barriuso et al. (2008)
4-Nitroguaiacol and quinoline promoter	<i>Pseudomonas simiae</i>	Soybean seed germination	Vaishnav et al. (2016)
Phytohormones as elicitor molecule	Cyanobacteria and cyanobacterial extracts	<i>Oryza sativa</i> , <i>Triticum aestivum</i> , <i>Zea mays</i> , <i>Gossypium hirsutum</i>	Singh (2014)
Reduction in Na ⁺ level and increase in K ⁺ level	<i>Pseudomonas koreensis</i> strain AK-1	<i>Glycine max</i> L. Merrill	Kasotia et al. (2015)
High hydraulic conductance, increased root expression of two ZmPIP isoforms	<i>Bacillus megaterium</i>	<i>Zea mays</i>	Marulanda et al. (2010)
High osmotic root hydraulic conductance due to increased active solute transport through roots	<i>Glomus intraradices</i> BEG 123	<i>Phaseolus vulgaris</i>	Aroca et al. (2007)
Increased root but decreased shoot proline concentrations	<i>Glomus etunicatum</i>	<i>Glycine max</i>	Sharifi et al. (2007)
Reduction of proline content	<i>Brachybacterium saurashtrense</i> , <i>Brevibacterium casei</i> , <i>Haererohalobacter</i> sp.	Peanut (<i>Arachis hypogaea</i>)	Shukla et al. (2012)
Increased accumulation of proline	<i>Burkholderia</i> , <i>Arthrobacter</i> , and <i>Bacillus</i>	<i>Vitis vinifera</i> , <i>Capsicum annuum</i>	Barka et al. (2006)
Phytohormone production and proline accumulation	<i>Azospirillum</i> sp. <i>B. aquimaris</i> SU8	Wheat (<i>T. aestivum</i>)	Zarea et al. (2012), Bal et al. (2013)

(continued)

Table 1.1 (continued)

Pathway	Bacteria	Plants	References
Accumulation of carbohydrates	<i>Glomus fasciculatum</i>	<i>Phragmites australis</i>	Al-Garni (2006), Porcel and Ruiz-Lozano (2004)
	<i>Glomus intraradices</i>	<i>Glycine ma</i>	
High stomatal conductance and photosynthesis	<i>Azospirillum brasilense</i> and <i>Pantoea dispersa</i> (co-inoculation)	<i>Capsicum annuum</i>	del Amor and Cuadra-Crespo (2012)
Decreased root and shoot Na ⁺ accumulation and enhanced root K ⁺ concentrations	<i>Glomus intraradices</i> BAFC 3108	<i>Lotus glaber</i>	Sannazzaro et al. (2006), Rabie (2005), Daei et al. (2009), Kaya et al. (2009)
		<i>Vigna radiata</i> .,	
	<i>Glomus clarum</i>	<i>Capsicum annuum</i> .,	
	<i>Glomus etunicatum</i>	<i>Triticum aestivum</i>	
Decreased root transcriptional expression of a high-affinity K ⁺ transporter (<i>AtHKT1</i>) decreasing root Na ⁺ import	<i>Bacillus subtilis</i>	<i>Arabidopsis</i>	Zhang et al. (2008)
Exopolysaccharide production, and reduced availability of Na ⁺ for plant uptake	Exopolysaccharide-producing bacteria, i.e., <i>Bacillus</i> , <i>Burkholderia</i> , <i>Enterobacter</i> , <i>Microbacterium</i> , <i>Paenibacillus</i>	Wheat (<i>T. aestivum</i>)	Ashraf and Harris (2004), Ashraf (2004), Kohler et al. (2006), Nadeem et al. (2010), Upadhyay et al. (2011), Aroca et al. (2008)
		Mung bean	
Reduced concentration of ABA	<i>Glomus intraradices</i> BEG121	<i>Lactuca sativa</i>	Aroca et al. (2008), Yao et al. (2010)
	<i>Pseudomonas putida</i> Rs-198	<i>Gossypium hirsutum</i>	
Stimulation of persistent exudation of flavonoids	<i>Azospirillum brasilense</i> strain Cd	<i>Phaseolus vulgaris</i>	Dardanelli et al. (2008)
Root-to-shoot cytokinin signaling and stimulation of shoot biomass	<i>Bacillus subtilis</i>	<i>Lactuca sativa</i>	Arkhipova et al. (2007)
Enhanced antioxidant responses through ROS-scavenging enzymes	<i>Bacillus safensis</i> , <i>Ochrobactrum pseudogregnonense</i> <i>Enterobacter</i> sp. UPMR1	Wheat (<i>Triticum aestivum</i>)	Chakraborty (2013), Habib et al. (2016)
		Okra	

(continued)

Table 1.1 (continued)

Pathway	Bacteria	Plants	References
Degrading ACC produced and therefore reduced elevated ethylene level	<i>Pseudomonas putida</i> , <i>Enterobacter cloacae</i> , <i>Serratia ficaria</i> , and <i>P. fluorescens</i>	Wheat (<i>T. aestivum</i>) <i>Catharanthus roseus</i>	Nadeem et al. (2013), Karthikeyan et al. (2012), Ali et al. (2014)
	<i>Achromobacter xylosoxidans</i>	Avocado (<i>Persea gratissima</i>)	
	<i>Arthrobacter protophormiae</i>		
	AUM54 <i>Pseudomonas fluorescens</i> YsS6	Rice (<i>Oryza sativa</i>)	
	<i>P. migulae</i> 8R6		
	<i>Bacillus</i> sp., <i>Variovorax</i> sp.		
	<i>Alcaligenes faecalis</i> , <i>Bacillus pumilus</i> , <i>Ochrobactrum</i> sp.		
Ascorbate peroxidase (APX), catalase (CAT), and glutathione reductase (GR) activity	<i>B. subtilis</i> , <i>Arthrobacter</i> sp.	Wheat (<i>T. aestivum</i>)	Upadhyay et al. (2012)
Biofilm, exopolysaccharide, and accumulated osmolytes	<i>Staphylococcus saprophyticus</i> (ST1)	<i>Lens esculenta</i> var. masoor 93	Arevalo-Ferro et al. (2005)
Nematodes carry more bacteria on their cuticle and increase colonization	<i>P. fluorescens</i> 10586, <i>P. fluorescens</i> SBW25	<i>Triticum aestivum</i> var. Savannah	Knox et al. (2003)
	<i>B. subtilis</i>		
	<i>P. corrugata</i>		
Increased stomatal conductance and transpiration rate	<i>B. drentensis</i>	Mung bean	Mahmood et al. (2016), Ahmad et al. (2013)
Phytohormone production	<i>P. extremorientalis</i> , <i>P. chlororaphis</i>	Common bean (<i>Phaseolus vulgaris</i>)	Egamberdieva et al. (2011)
Production of gluconic acid, ACC deaminase, phytohormones	<i>P. pseudoalcaligenes</i> , <i>B. pumilus</i>	Rice (<i>O. sativa</i>)	Jha et al. (2013), Rojas-Tapias et al. (2012)
	<i>Azotobacter chroococcum</i>	Maize (<i>Z. mays</i>)	
Indolyl-3-acetic acid (IAA) and auxin increased	<i>Streptomyces</i> sp.	Wheat (<i>T. aestivum</i>)	Sadeghi et al. (2012)
Reduced production of ethylene and increased uptake of phosphorous and potassium	<i>Achromobacter piechaudii</i>	Tomato (<i>L. esculentum</i>)	Mayak et al. (2004)

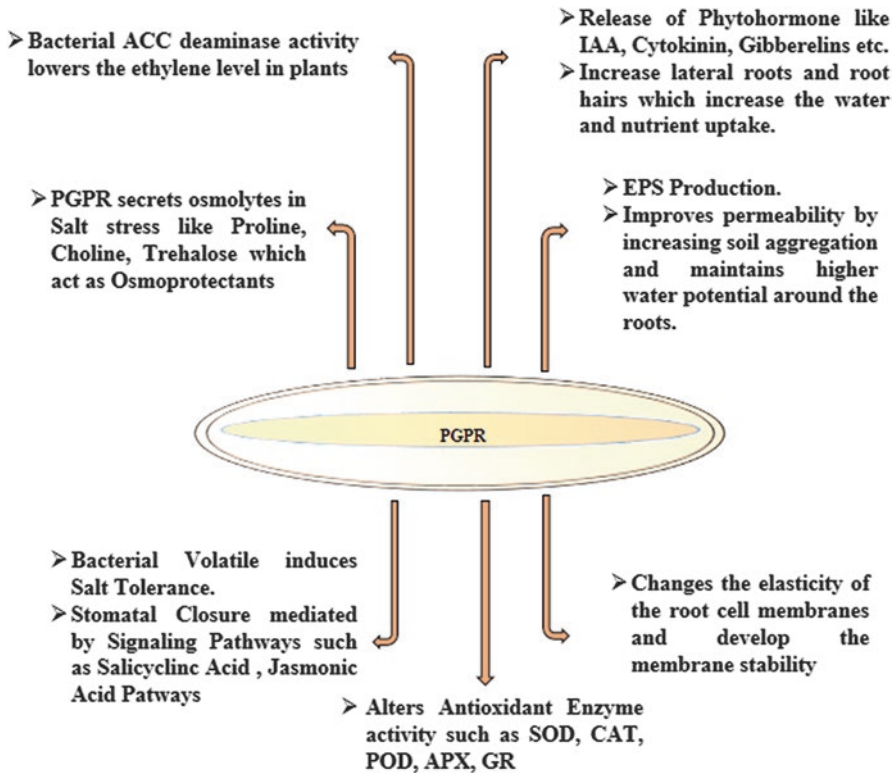


Fig. 1.1 Mechanism of plant salt tolerance induced by plant growth-promoting rhizobacteria (PGPRs)

ROS detoxification, protection of membrane integrity, and enzyme/protein stabilization (Hayat et al. 2012). Very important compatible solutes are proline, ectoine, trehalose, polyols, and sucrose and quaternary ammonium compounds (QACs) such as glycine betaine, proline, alanine, and percolate.

Accumulation of these osmolytes in bacteria and plants is an indicator of salt tolerance in response to salt stress (Bremer 2000; Gul et al. 2013). Many species of bacteria respond to increase in osmotic pressure by accumulating osmoregulatory solutes, so-called compatible solutes, up to high intracellular concentrations for coping with high external salinity. In many halophytes, proline or glycine betaine occurs at sufficiently high concentrations in leaves to compensate the osmotic stress on the cell. The concentration of compatible solutes rise up to 40 mM/tissue water when the osmotic pressure rises above 0.1 MPa (Flowers et al. 1977). To maintain turgor pressure in highly saline environments, considerable concentrations of solutes need to be accumulated in the cells (Imhoff 1986).

1.7 Proline as an Influential Compatible Solute for Stress Responses After PGPR Inoculation

Plants usually produce substantial amount of various compatible organic solutes under stress conditions, most commonly proline and glycine betaine (Serraj and Sinclair 2002). Proline as an osmoprotectant was discovered first in bacteria, and the relationship between proline accumulation and salt tolerance was also noticed (Csonka et al. 1988; Csonka and Hanson 1991). A wide variety of bacteria and plants respond to osmotic stress or dehydration by increasing their cellular proline levels. Proline accumulation is a sensitive physiological index for the response of plants to salt and other stresses (Liang et al. 2013) to maintain higher leaf water potential and to keep plants protected against oxidative stress (Lutts et al. 1999). On the other hand, proline also stabilizes many functional units such as ribulose biphosphate carboxylase/oxygenase (RUBISCO) enzymes and complex II electron transport (Mäkelä et al. 2000). Proline helps the plant cell to alleviate salt stress by stabilizing subcellular structures like proteins and membranes (Huang et al. 2009). Proline also helps in scavenging free radicals and buffering cellular redox potential (Ashraf and Foolad 2007; Kohler et al. 2009). Increased total soluble sugar (TSS) content of plants under salinity stress is another vital defense strategy to cope with salinity stress. An increased amount of proline and total soluble sugar in wheat plants inoculated with PGPR significantly contributed to their osmotolerance (Upadhyay et al. 2012).

It is suggested that proline accumulation is a symptom of salt stress injury in rice and that its accumulation in salt-sensitive plants results from an increase in ornithine- δ -aminotransferase (OAT) activity and an increase in the endogenous pool of its precursor glutamate (Mansour and Ali 2017). Proline concentration in leaves, stems, and roots will increase under salt stress conditions. Proline also acts as a signaling molecule for antioxidative defense pathway and has metal chelating activity. The enzymes Δ^1 -pyrroline-5-carboxylate synthetase (P5CS) and Δ^1 -pyrroline-5-carboxylate reductase (P5CR) are responsible for proline biosynthesis from its precursor, glutamate. The other pathway to synthesize proline is from ornithine, which is converted via ornithine- δ -aminotransferase (OAT) to γ -glutamate-semialdehyde (GSA) into Δ^1 -pyrroline-5-carboxylate (P5C) (Liang et al. 2013). The enzymes proline dehydrogenase (PDH) and P5C dehydrogenase (P5CDH) catabolize proline back to glutamate.

1.7.1 Proline Biosynthesis Under Stress Order

Ubiquitous pathway for proline biosynthesis is to derive glutamate via phosphorylation to γ -glutamyl phosphate by the activation of the γ -glutamyl kinase enzyme. The biosynthesis of proline from glutamate is catalyzed by three enzymatic reactions which are catalyzed by γ -glutamyl kinase (GK; proB product), γ -glutamyl phosphate reductase (proA product), and Δ^1 -pyrroline-5-carboxylate reductase (proI product). In general, proI on the chromosome is so distant from the operon

constituted by *proB* and *proA* genes. Three proline transport systems including proline permease gene (PutP), ProP, and ProU were possessed by gram-negative bacteria *E. coli* and *S. typhimurium* (Sleator and Hill 2002). Proline was individually transported as a carbon or nitrogen source by PutP system (Sleator and Hill 2002), which plays little role in osmoadaptation. The PutP is a high affinity system which has significant homologies with PutP of *E. coli*, which is responsible for transporting proline in the cellular system. Proline was uptaken by this system, which acts independently to osmotic stimulation.

Proline accumulation in plants under stress condition usually occurred from two different precursors, glutamate and ornithine. Proline converted from glutamate is the first pathway, which involves two successive reductions: catalyzed (i) pyrroline-5-carboxylate synthase (P5CS) and (ii) pyrroline-5-carboxylate reductase (P5CR), respectively. P5CS is a bifunctional enzyme catalyzed first from the activation of glutamate by phosphorylation and second the reduction of the labile intermediate γ -glutamyl phosphate into glutamate semialdehyde (GSA), which is in equilibrium with the P5C form (Hu et al. 1992). Mitochondrial enzyme ornithine is an alternative precursor for Proline biosynthesis. It can be transaminated by ornithine- δ -amino transferase (OAT) to P5C. Glutamate pathway is the central pathway during osmotic stress. However, in young *Arabidopsis* plants, the ornithine pathway seems to contribute, and δ -OAT activity is enhanced (Roosens et al. 1998).

1.7.2 Proline Degradation

Proline degradation is a rate-determining step of its pathway similar to proline biosynthesis. Proline can be degraded by proline dehydrogenase (PDH) and P5C dehydrogenase (P5CDH) enzymes. Proline degradation takes place in the mitochondria, while biosynthesis occurs in the cytosol and the plastids of the green tissues (e.g., chloroplasts) (Elthon and Stewart 1981; Rayapati et al. 1989; Szoke et al. 1992). Most of the plants like *Arabidopsis* have two functional Proline dehydrogenase (PDH) isoforms, (i) Proline dehydrogenase-1 (PDH1) and (ii) Proline dehydrogenase-2 (PDH2), which are localized in the mitochondria (Funck et al. 2010; Kiyosue et al. 1996). PDH1 is predominant isoform in plant and present in higher amount than PDH2. It is mainly expressed in the vasculature of leaves (Funck et al. 2010). Funck et al. (2010) suggested that proline degradation in the vasculature may provide essential energy for the plant during stress exposure.

Proline acts as a vital energy source for recovery phase under salinity stress (Szabados and Savoure 2010; Hare and Cress 1997). The salient feature of proline catabolism is to drive the oxidative phosphorylation in plants. The PDH1 mutant *Arabidopsis* showed significantly lower oxygen consumption in the root apex (Sharma et al. 2011). The recovering tissues in mitochondria get help to drive oxidative phosphorylation and ATP synthesis from proline oxidative metabolism. PDH and P5CDH expression are similarly increased during stress recovery phase (Kiyosue et al. 1996).

1.7.3 Importance of Proline to Alleviate Stress

In response to environmental stress, proline is accumulated naturally in plants similar to other microorganisms including protozoa and algae and bacteria (Csonka 1981a; Matysik et al. 2002; Szabados and Savoure 2010; Verbruggen and Hermans 2008). Plants recover from stress condition by the accumulation of proline as a signaling molecule. Proline can leverage cell proliferation or cell death and mitochondrial stress functions and regulate specific gene expression. Genetic modification of proline metabolism could escort new opportunities to boost plant tolerance from environmental stresses. The intracellular proline levels have been increased by more than 100-fold in plants during stress (Handa et al. 1983; Verbruggen and Hermans 2008). The plants tend to accumulate proline during salt stress (Yoshiba et al. 1995), drought stress (Barnett and Naylor 1966; Choudhary et al. 2005), heavy metal stress (Chen et al. 2001), UV radiation exposure (Saradhi et al. 1995), pathogen infection (Fabro et al. 2004) and oxidative stress (Yang et al. 2009). Exo- and endogenously manipulating proline levels (Hare et al. 1999) under stress conditions in plants involve reciprocal regulation of P5CS and PDH (Liang et al. 2013). Overexpression of P5CS in tobacco results in higher levels of proline, enhanced osmotolerance, flower development, and increased root biomass (Hare et al. 1999; Hong et al. 2000). Proline plays a vital role in scavenging hydroxyl radicals (Smirnoff and Cumbes 1989), chelating heavy metals (Farago and Mullen 1979), and reducing metal uptake (Wu et al. 1998) in the cytoplasm.

Proline has since been shown to accumulate high intracellular concentrations in a variety of bacteria, following exposure to osmotic stress (Measures 1975). Intracellular proline pool of many gram-positive bacteria has been shown to increase by cellular biosynthesis (Cayley et al. 1992; Whatmore and Reed 1990), whereas gram-negative bacteria achieve higher proline concentration by enhanced transport system during osmotic stress (Sleator and Hill 2002). Proline has been accounted as the most substantial part of amino acid accumulation in response to osmotic stress for gram-negative and gram-positive bacterial strains (Imhoff 1986; Hua et al. 1982). The intracellular proline level was elevated with increase in osmolarity of the medium (Perroud and Le Rudulier 1985; Imhoff 1986).

The primary response to high salinity in bacterial cell (*E. coli*) is the accumulation of K^+ and glutamate. The K^+ accumulation in the cell takes place through the action of Kdp (ion-motive P-type ATPase) and Trk (Potassium transport proteins) system (Sasaki et al. 2013). The accumulation of proline or glycine betaine in the cytosol upregulates the activity of Kef system (Potassium efflux system) which in turn depletes the glutamate pool (Sasaki et al. 2013). In various non-halophilic bacteria, the total amino acid pool increases with the increase in external osmolarity, and specifically it was noticed that proline accumulation is significant (Imhoff 1986). In general, bacterial species which accumulate proline are more salt tolerant than those which do not. Accumulation of osmolytes in bacterial strains at higher salinity might be involved for their adaptation to saline environments in the soil for improving plant growth.