

Mohd Sayeed Akhtar *Editor*

Salt Stress, Microbes, and Plant Interactions: Mechanisms and Molecular Approaches

Volume 2

 Springer

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Editor

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*This book is dedicated to my grandfather,
Nana*



Muhammad Aziz-ur-Rahman (1907–1985)

*A great scholar, statesman, social reformer;
and famous hakim of the twentieth century*

Foreword



Global warming and other potential climatic abnormalities associated with it cause different types of biotic and abiotic stress conditions that lead to affect plant growth and yield severely. Though not visible to our naked eyes, plant-microbe interactions occur in several ways. In fact, plant interacts with microbes at a certain phase of their life, and this communication is not inevitably harmful for the plant. Indeed, there are copious examples of plant-microbe associations that effectively benefit the plants by enhancing their growth, survivability, and productivity. The plant-microbe interaction is very essential for combating any stressful conditions. The microbes associated with plants secrete volatile compounds that encourage plant growth and/or provide resistance against abiotic and/or biotic stresses. Microorganisms, occupying in different environments, have variable biological and metabolic mechanisms to overcome ecological stresses. As the microbial diversity in the environment is very high, it is required to characterize and clarify microbial associations with plants in relation to protect them against several ecological encounters. The microbiota of different soils and their beneficial effect on plants need to be studied in detail, so that they can be used as a consortium to improve crop productivity under different agro-climatic conditions. Moreover, understanding the physiological and molecular mechanisms involved in plant-microbe interactions will be very useful for improving the agronomic applications of rhizospheric microbes. The recent advancements in modern techniques have helped in identifying and quantifying the microbial diversity linked with plants. This has allowed us to understand the immense interactions of microbes with the plants. The knowledge of these research

accomplishments provides a comprehensive understanding on multidimensional communications between microbes and plants. Thus, it is required to have a collective database on the existence of varied stress combinations in agronomically important areas, and this will allow one to make use of the beneficial microbes to provide stress tolerance.

The present volume to be published by “Springer,” *Salt Stress, Microbes and Plant Interactions: Mechanisms and Molecular Approaches* (Volume 2), includes 13 chapters contributed by the authors from different parts of the world. Chapter 1 by the Indian authors provides information on the role of microbes in the management of crop salinity. Also, it discusses on the mechanisms and microbial applications in overcoming salinity stresses. Chapter 2 contributed by the Malaysian authors describes in detail about the adaptive mechanisms of plant responses to salts. In Chaps. 3 and 4, the Indian authors have summarized the molecular approaches and salt tolerance mechanisms in leguminous plants and crop improvement through microbial biotechnology. In Chapter 5, the Indian authors discuss the role of phytohormones in recuperating salt stress. Similarly, Chaps. 6 and 7 by the Malaysian and Indian authors, respectively, describe the genetic responses of plants to salt stresses and the use of microbial biotechnology in improving salt stress and crop productivity. Chapter 8 discusses the consequences of bioinoculants and intercropping approach to alleviate salinity stresses. However, Chap. 9 entails the pathways of signaling molecules in improving salt stress in plants. Chapter 10 by the Indian authors describes the mechanisms and molecular approaches for salt tolerance enhancement. Similarly, Chaps. 11 and 12 by Pakistani contributors describe the methods used to reduce and mitigate the adverse impact of soil salinity and to overcome salt stresses through bacterial inoculation. Lastly, Chap. 13 by the Indian authors describes the diverse roles of proline and its mechanism of tolerance and adaptation under salinity stress. In this edited volume, an attempt has been made to highlight both the hypothetical and practical aspects of salt stress tolerance in plants. Furthermore, it highlights on the physiological, ecological, biochemical, and molecular mechanisms involved in various plant-microbe interactions to overcome salt stresses. I personally congratulate Dr. Mohd Sayeed Akhtar for his noble academic efforts in bringing out this book volume.

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Mallappa Kumara Swamy

Preface



Salt stress has pessimistic crash on the yields of various agricultural crops, and it may directly affect the livelihood of farmers worldwide. The excessive salts in soil lower the availability of water, inhibit metabolic processes, and affect nutrient composition, osmotic balance, and hydraulic conductivity that result to stunted growth and low productivity of cultivated crop plants. Plants have developed number of processes involved in the tolerance mechanism, such as various compatible solutes, polyamines, reactive oxygen species and antioxidant defense mechanism, ion transport, and compartmentalization of injurious ions. To overcome this problem, the exploitation of genetic variation; the use of plant hormones, mineral nutrients, and soil microbes; and other mechanical practices are of prime importance. It is a fascinating subject, which is multidisciplinary in nature, and concerns scientists involved in plant heath. There have been marked advances in this field during the past few decades.

Salt Stress, Microbes, and Plant Interactions: Mechanisms and Molecular Approaches (Volume 2) is a very timely effort in this direction. This book volume describes both the theoretical and practical aspects of salt stress tolerance and the physiological, ecological, biochemical, and molecular mechanisms involved in

understanding these multi-tropic interactions. I hope that the book will be helpful to graduate students, teachers, researchers, and industry persons who are interested in agronomy, ecology, stress physiology, environmental science, crop science, and molecular biology.

I am highly grateful to all our contributors for readily accepting our invitation, for not only sharing their knowledge and research but also venerably integrating their expertise in dispersed information from diverse fields in composing the chapters, and for enduring the editorial suggestions to finally produce this venture. I greatly appreciate their commitments. I am also thankful to Professor Mallappa Kumara Swamy for his suggestion and for writing the foreword of this volume. Moreover, I am thankful to my beloved wife, Mrs. Shagufta Bano, and lovely sons, Mohd Rafeen and Mohd Almaan, for their unconditional encouragement, support, and moral boost up throughout the compilation of this book volume. I also thank the team of Springer Nature, especially Dr. Kapila Mamta, Raman Shukla, and Raagapriya Chandrasekaran, for their generous cooperation at every stage of the publication.

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Mohd Sayeed Akhtar

About the Book

The interaction between plant, soil, and microbes is fairly intricate and is essential for combating any stressful condition. The presence of excessive salt in soil lowers the availability of water, inhibits metabolic processes, and affects nutrient composition, osmotic balance, and hydraulic conductivity that resulted in the stunted growth and lower productivity of crop plants. *Salt Stress, Microbes and Plant Interactions: Mechanisms and Molecular Approaches* (Volume 2), along with the recently published *Salt Stress, Microbes and Plant Interactions: Causes and Solution* (Volume 1), provides a detail account on the physiological, ecological, biochemical, environmental, and molecular levels for this multi-tropic interaction. Specifically, these two titles are focus on both the theoretical and practical aspects and also provide a solid foundation for students, teachers, researchers, and industry persons interested in agronomy, ecology, stress physiology, environmental science, crop science, and molecular physiology.

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About the Editor

Dr. Mohd Sayeed Akhtar (PhD) is working as an assistant professor in Gandhi Faiz-e-Aam College, Shahjahanpur, UP, India. He has received his PhD degree from Aligarh Muslim University (AMU), India, in 2008, prior to conducting postdoctoral research at the Botanical Institute, University of Basel (BIB), Switzerland, in 2008–2010, and Chonbuk National University (CBNU), Republic of Korea, in 2011. He was an assistant professor at Jimma University, Ethiopia (2011–2014), and a fellow researcher at the International Institute of Tropical Agriculture, Universiti Putra Malaysia (UPM) (2014–2015). He has more than 15 years of research and 10 years of teaching experience in soil microbiology, applied microbiology, environmental microbiology, molecular biology, plant pathology, and plant nanobiotechnology. He is author and coauthor of more than hundred articles in peer-reviewed journals, conference proceedings, and book chapters and has edited 12 books with international publishers. He is serving the scientific community as editorial board member and reviewer of several high-impact international journals. His current research is focused on the rhizospheric plant-microbe interactions and their molecular biotechnology, bioremediation, biomineralization, nano-fertilizers, and nanobiotechnology.



Microbial Management of Crop Salinity Stress: Mechanisms, Applications, and Prospects

1

Hillol Chakdar, Dnyaneshwar Namdev Borse,
Shaloo Verma, Prassan Choudhary, and Sudipta Das

Abstract

Salinity stress is a major deterrent to crop growth worldwide. A high concentration of salt in soil and irrigation water reduces water uptake by plants, which triggers a range of cellular and metabolic processes ultimately resulting in lowered crop yield. Genetics of salinity tolerance in plants is well understood and has been successfully utilized to breed improved crop varieties; however, such strategies are long drawn and cost intensive. Microorganisms due to their immense metabolic diversity can be very useful to devise low-cost strategies to ameliorate salinity stress in crop plants. An intricate and highly complex interaction between plant and microbe results in alleviation of salt stress. Although the cross talk between the plant and microbe is not clearly understood, regulation of osmotic balance and ion homeostasis by microorganisms are mostly mediated through modulation of phytohormone production, alteration in gene expression, protein function, and metabolite synthesis in plants. Consequently, improved antioxidant activity, accumulation of compatible solutes, proton extrusion mechanism, salt compartmentalization, and improved nutrient status in plants can reduce the osmotic shock and ionic toxicity. Microbial management of salt stress offers an eco-friendly, cost-effective approach which however requires a rigorous selection, testing, and validation of the microbial strain(s) besides understanding the cross talk between the plant and microbe. Therefore, the aim of this chapter is to discuss the salinity response in plants and also to understand the mechanisms of microbe-mediated salinity stress alleviation on the molecular basis.

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Keywords

Salinity · Plant-microbe interaction · Osmolytes · Antioxidants · Gene expression
· Phytohormone · ACC deaminase

1.1 Introduction

Soil salinity has become a major constraint in agriculture as high salt content in soils restricts crop growth and reduces yield. The saline soils are characterized with high concentration of soluble salts with an electrical conductivity (EC) $>4 \text{ dS m}^{-1}$ and exchangeable sodium percentage <15 . Salt concentration of saline soils is more than 40 mM NaCl equivalent which generates an osmotic pressure of more than 0.2 MPa (Sharma et al. 2016). Major causes of natural soil salinity have been attributed to salt water intrusion and deposition of salts through wind. However, poor soil drainage, irrigation with highly saline water, improper irrigation, and excessive use of manures/composts have also been shown to increase salinity of soils (Kotuby-Amacher et al. 2000). Worldwide saline soils cover approximately 260 Mha with most extensive soil salinity reported in the arid and semi-arid regions of North Africa, the Near East, the former Soviet Union, and Central Asia (Cherlet et al. 2018). Osmotic pressure of soil solution increases due to high salt concentration which in turn adversely affects plant growth by reducing water uptake and balanced absorption of essential nutrients (Tester and Davenport 2003). Reduced uptake of water and nutrients hampers major metabolic functions of plant cells which ultimately affect germination, plant vigor, and crop yield (Munns and Tester 2008). Salinization in root zone may cause yield reduction to the tune of 30% (Cherlet et al. 2018). About 30 species of crop plants provide ~90% of plant-based human food which under moderate salinity reduce average yields by 50–80% (Panta et al. 2014). Annually the loss in crop production due to salt-induced land degradation globally costs approximately US\$ 27.3 billion (Cherlet et al. 2018).

Globally researchers are making huge efforts to develop salinity-tolerant varieties to combat the ill effects of salinity on crop production, but only very little success has been achieved (Munns and Tester 2008). Sustainable, eco-friendly, and low-cost management practices for successful reclamation of saline soils for crop production have become a challenge for the researchers and policy makers. Microorganisms due to their multiple plant beneficial functions and ability to adapt to a wide range of environmental conditions have long been used in agriculture. Many of such plant beneficial microorganisms can be useful to crop plants for their better growth and sustenance under saline conditions. Microbes have been reported to alleviate salinity stress to plants through production of phytohormones, repressing production of stress hormones, enhancing plant stress defense mechanisms, improving plant nutritions, etc. Soil microflora and endophytes have an intricate interaction with agricultural plants to maintain productivity under stressed

conditions. Microorganisms from hypersaline environments, halophytes represent a unique biological resource for salinity alleviation. Microbiologists and environmental scientists are putting huge efforts to bring out low-cost microbial technologies for salinity amelioration in crop plants. Published reports show the potential of such technologies, but still their large-scale application in agriculture is yet to be materialized globally. Therefore, the aim of this chapter is to discuss the salinity response in plants and also to understand the mechanisms of microbe-mediated salinity stress alleviation on the molecular basis.

1.2 Effect of Soil Salinity on Plant Growth and Productivity

High salt concentration in soils limits agricultural productivity by exerting negative effects on germination, seedling growth, development of root, flowering, and fruit setting (Fig. 1.1a, b) (Alam et al. 2004; Munns and Tester 2008). When concentration of solutes in root zone increases, the water potential of soil decreases. Reduced soil water potential hinders plant in maintaining turgor and thereby limits the water uptake. Broadly, salinity affects growth of plants in the following ways, viz., (a) imposing osmotic stress through reduced soil water potential; (b) inducing ionic imbalance in cells, specifically reducing the concentrations of K^+ , Ca^{2+} , and NO_3^- , and causing ion (Na^+ and/or Cl^-) toxicity; and (c) creating oxidative stress (Zeng et al. 2015). During the salinity stress in plants, a number of biochemical and physiological changes take place within the cells and tissues.

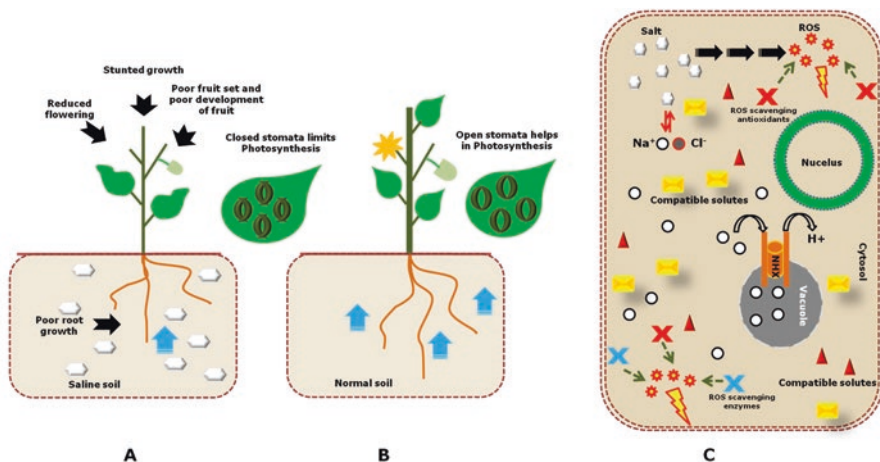


Fig. 1.1 Diagrammatic representation of (a) poor stunted growth and development of plant under saline soil, (b) healthy plant growth under normal soil, and (c) different cellular mechanisms acting to combat salinity stress

1.2.1 Biochemical Changes

1.2.1.1 Osmotic Stress

Higher amount of salts in root zone decreases soil water potential leading to reduced water uptake. Further, plant growth reduces due to toxic accumulation of Na^+ which occurred in leaves (Munns 2005; Munns and Tester 2008; Rahnema et al. 2010). Osmotic shock results in disrupted membrane permeability, reduced relative water content, leaf water potential, transpiration rate, water retention, and water-use efficiency (Munns 2002). Due to reduced soil water potential, the plants are unable to maintain turgor pressure resulting in stomatal closure leading to reduced photosynthetic activity.

1.2.1.2 Specific Ion Toxicity

Plants under salinity stress accumulate higher amounts of sodium, chloride, sulfate, and bicarbonate ion leading to severe ion toxicity. It is known that toxic accumulation of Na^+ takes place more rapidly than Cl^- (Munns and Tester 2008). Toxicity to a specific ion varies with different plant species (Dogan et al. 2010). Ion toxicity may cause changes in the metabolic processes taking place in the cytoplasm and may exert damaging effects on photosynthesis (White and Broadley 2001).

1.2.1.3 Nutritional Imbalance

Salinity can differentially affect the mineral nutrition of salt-stressed plants through nutritional deficiency or imbalance due to the competition of Na^+ and Cl^- with K^+ , Ca^{2+} , NO_3^- , and Mg^{2+} (Karimi et al. 2005). Nutrient imbalance under salinity reduces plant growth by affecting the availability, transport, and partitioning of nutrients.

1.2.1.4 Reactive Oxygen Species (ROS)

The primary effects of salinity give rise to a number of secondary effects like oxidative stress due to buildup of reactive oxygen species (ROS) in plant cell (Mittler 2002; Abbasi et al. 2014). High salinity results in increased peroxidation of membrane lipids leading to membrane leakage (Ahmad et al. 2015). Overproduction of ROS enhances protein degradation and DNA mutation along with membrane injury (Pitzschke et al. 2006; Porcel et al. 2012).

1.2.2 Physiological Changes

1.2.2.1 Water Relations

High concentration of salts reduces water and osmotic potential of plants and thereby increases the turgor pressure (Meloni et al. 2001; Romero-Aranda et al. 2001; Gulzar et al. 2003). Under high salt concentration, increase in NaCl within the leaf tissue results in lower osmotic and water potentials. Similarly, transportation of water from roots to the shoots reduces with the reduction in root hydraulic conductance causing water stress in the leaf tissue.

1.2.2.2 Membrane Stability

Due to increased accumulation of Na^+ inside the cell, plants suffer from membrane destabilization and disrupt the membrane of different organelles: vacuole, chloroplast, mitochondria, and endoplasmic reticulum.

1.2.2.3 Leaf Anatomy

Salinity is known to induce anatomical changes in leaves like reduced leaf area and chlorophyll content, faster defoliation, stomatal resistance, photosynthetic activities, etc. (Shannon et al. 2000; Zhang et al. 2016). Thicker epidermis, mesophyll, longer and wider palisade cells, and larger spongy cells under high salinity have been reported (Parida et al. 2004). Under high salinity, reduced intercellular spaces were observed in spinach leaves, while stomatal density reduced in tomato leaves (Delfine et al. 1998; Romero-Aranda et al. 2001).

1.2.2.4 Photosynthesis

Due to osmotic stress and partial closure of stomata, photosynthetic capacity is reduced in many plant species (Ashraf 2001; Kao et al. 2001; Romero-Aranda et al. 2001; Meloni et al. 2003). Salt injury to photosystem II (PSII) is widely reported (Tavakkoli et al. 2011); this in turn contributes to inhibition of photosynthesis. After closure of stomata, activity of a number of enzymes including RuBisCo is reduced due to internal reduction of CO_2 and thus limiting carboxylation and reducing the net photosynthetic rate (Chaves et al. 2009).

1.3 Overview of Mechanism of Salinity Tolerance in Plants

In response to salinity stress, plants exhibit a number of physiological and biochemical strategies to cope with the stress (Fig. 1.1c). The strategies used by plant are briefly described below.

1.3.1 Accumulation of Osmoprotectant/Compatible Solutes

Osmotic adjustment of cell is vital for sustenance under salinity stress. Plants synthesize a number of osmolytes (also known as compatible solutes) to maintain the osmotic balance. Low molecular weight sugars, organic acids, polyols, amino acids, amides, imino acids, ectoine, proteins, and various quaternary ammonium compounds (QACs) are generally known to act as compatible solutes in plants (Suprasanna et al. 2005). Under high salinity, compatible osmolytes accumulate in plant tissues to help plants to survive during hostile condition through osmotic adjustment, stabilization of proteins, and detoxification of reactive oxygen species (Ahangar et al. 2014; Slama et al. 2015). Soluble sugars like trehalose, sucrose, fructose, etc. are well known as osmolyte and osmoprotectant. Under salt stress, amino acids like proline accumulates in higher plants (Mansour 2000). Proline is osmotically very active; it mitigates the effect of NaCl on cell membrane disruption

(Hossain et al. 2011) and maintains membrane stability (Nounjan et al. 2012) by regulating the accumulation of useable N acting as energy and nitrogen reserve during salinity (Tahir et al. 2012). Under salt stress compatible quaternary ammonium compounds (QACs) like glycinebetaine, alaninebetaine, prolinebetaine, choline *O*-sulfate, hydroxyprolinebetaine, and pipercolatebetaine are synthesized and accumulate in plant cells (Mansour 2000). Glycinebetaine (GB) is the most abundant osmoprotective QAC found in chloroplasts and plays an important role in osmotic adjustment and protection of thylakoid membranes, thereby maintaining photosynthetic efficiency, and protection of cellular macromolecules. Polyamines also significantly contribute in salt stress tolerance. Acyclic polyol (mannitol, glycerol, sorbitol) and cyclic polyol (ononitol and pinitol) are known to accumulate in plants during salt stress.

1.3.2 Ion-Selective Absorption and Compartmentalization to Protect from Ion Toxicity

During salinity stress, influx of Na^+ in cells results in ionic imbalance. Plant salinity tolerance is associated with the decreased loading of Na^+ into xylem resulting in exclusion of the Na^+ from shoots (Garthwaite et al. 2005; Munns and Tester 2008). Salt-stressed plants can maintain ionic balance through restricting toxic ion uptake, maintaining the uptake of essential ions, and compartmentalizing toxic ions to vacuoles. Buildup of toxic levels of salts in shoots can be achieved by restricting entry of Na^+ into root cells and then into the transpirational stream. Expulsion of Na^+ from root cells is an important mechanism preventing accumulation of Na^+ within cells and further movement to shoots. Na^+/H^+ antiporters in cell membrane pump out Na^+ from root cells. The cytosolic Na^+ concentration is regulated by compartmentation (Bassil and Blumwald 2014). Vacuolar Na^+/H^+ antiporters (NHXs) compartmentalize Na^+ into the vacuoles, thereby lowering the chances of toxicity and also contributing to osmoregulation.

1.3.3 Scavenging of Reactive Oxygen Species to Protect from Oxidative Stress

ROS produced under stress leads to oxidative damage to constituent lipids of cell membrane, proteins, and nucleic acids. Removal of ROS from cells is a major mechanism used by plants to cope up stress. The antioxidant defense system through scavenging ROS plays an important role in plant adaptation to salinity stress (Ahangar et al. 2014). Plant produces different antioxidants and detoxifying enzymes for efficient removal of ROS. Ascorbate, glutathione reductase (GR), glutathione *S*-transferase (GST), α -tocopherol, carotenoids, etc. are some of the prominent antioxidants deployed by plants, while superoxide dismutase (SOD), catalase (CAT), peroxidase, and enzymes of the ascorbate-glutathione cycle are the major detoxifying enzymes. SOD converts superoxide to H_2O_2 , which is broken down to

water and oxygen by the catalase and/or ascorbate-glutathione cycle or by ascorbate peroxidase located in the thylakoid membrane of chloroplast (Wu et al. 2014). Nitric oxide (NO), which is a small volatile gaseous molecule, is also known to be involved in protecting oxidative damage of cellular machineries. NO reacts with lipid radicals, thus preventing lipid oxidation, exerting a protective effect by scavenging superoxide radical (Bajguz 2014).

1.4 Microorganisms in Salt Stress Alleviation in Crop Plants

Due to enormous metabolic diversity and unique ability to sustain under extreme conditions, microorganisms inhabiting the plant rhizosphere play an important role in alleviation of various stress factors including salinity in crop plants. The rhizosphere-inhabiting microorganisms are integral part of biogeochemical cycling of nutrients. They can stimulate plant growth through mobilization of nutrients in soils, production of phytohormones, conferring protection to plants from pathogens through production of antibiotics or other secondary metabolites, improving soil structure, sequestration of toxic chemicals or metals from soil, etc. A number of bacteria from diverse genera such as *Bacillus*, *Paenibacillus*, *Pseudomonas*, *Klebsiella*, *Pantoea*, *Azotobacter*, *Azospirillum*, *Microbacterium*, *Streptomyces*, etc. have been characterized as plant growth-promoting bacteria. Inoculation of such bacteria in plants has been proved to be beneficial for many crop plants. Under saline conditions, the microorganisms can be effectively used for alleviation of salinity stress. Under salinity stress, microorganisms can help plants to maintain the osmotic balance, reduce ROS accumulation, and improve nutrient mobilization which in turn helps to combat the stress. Saline/hypersaline environments or halophytes represent specifically adapted microorganisms and also offer a unique source of salinity stress alleviating microorganisms. Halotolerant bacteria due to their ability to tolerate high concentration of salt have the ability to rapidly proliferate in soils having variable degree of salinity. Such halotolerant bacteria with multiple plant growth-promoting traits have largely been reported to alleviate salinity stress in various plants (Table 1.1). Apart from halotolerant bacteria, arbuscular mycorrhizal (AM) fungi have also been reported to improve the salinity tolerance in some plants. For example, the co-inoculation of *R. intraradices* and *Massilia* sp. RK4 can restore root colonization by AM fungi and nutrient accumulation in maize plants during salinity stress. Such associations of fungi and microbes have significant impact on tolerance of salinity in maize (Krishnamoorthy et al. 2016). Some examples of AM fungi-mediated salinity alleviation are presented in Table 1.1.

1.4.1 Microbial Production and Modulation of Phytohormones for Salinity Tolerance in Plants

Phytohormones of microbial origin can evoke several physiological responses to the plants. Microorganisms are known to produce several phytohormones like indole

Table 1.1 Examples of some halophyte and rhizosphere-associated microorganisms involved in alleviation of salinity stress

Halotolerant bacteria associated with halophytes				
Halotolerant bacteria	Host halophyte	PGP activity	Plant response	References
<i>Bacillus</i> , <i>Pantoea</i> , <i>Marinobacterium</i> , <i>Acinetobacter</i> , <i>Enterobacter</i> , <i>Pseudomonas</i> , <i>Rhizobium</i> , and <i>Sinorhizobium</i>	<i>Psoralea corylifolia</i>	IAA production and siderophore production	Enhanced seed germination and root length of wheat	Sorty et al. (2016)
<i>Bacillus alcalophilus</i> , <i>B. thuringiensis</i> , and <i>Gracilibacillus saliphilus</i>	<i>Arthrocnemum macrostachyum</i>	IAA production, siderophore production, and phosphate solubilization	Mitigated the effects of high salinity on plant growth and physiological performance	Navarro-Torre et al. (2017)
<i>Dietzia natronolimnaea</i> STR1	Not reported	–	Increased wheat tolerance to salt stress by improved wheat growth in terms of plant dry weight and plant height (higher biomass, shoot, and root elongation), increased photosynthetic pigments, enhanced content of enzymes catalase and ascorbate peroxidase, and increased the gene expression of the antioxidants compared to uninoculated plants	Bharti et al. (2016)

(continued)

Table 1.1 (continued)

Halotolerant bacteria associated with halophytes				
Halotolerant bacteria	Host halophyte	PGP activity	Plant response	References
<i>Micrococcus yunnanensis</i> , <i>Planococcus rifietoensis</i> , and <i>Variovorax paradoxus</i>	Seven species of halophytes	N ₂ fixation, IAA production, siderophore production, phosphate solubilization, and ACC deaminase activity	An increase in salt stress tolerance, seed germination (%), and plant biomass, and photosynthetic capacity, and a decrease in stress-induced ethylene production at different NaCl concentrations (50–125 mM)	Zhou et al. (2017)
<i>Brachybacterium saurashtrense</i> sp. nov., <i>Zhihengliuella</i> sp., <i>Brevibacterium casei</i> , <i>Haererehalobacter</i> sp., <i>Halomonas</i> sp., <i>Vibrio</i> sp., <i>Cronobacter sakazakii</i> , <i>Pseudomonas</i> spp., <i>Rhizobium radiobacter</i> , and <i>Mesorhizobium</i> sp.	<i>Salicornia brachiata</i>	N ₂ fixation, IAA production, phosphate solubilization, and ACC deaminase activity	Increase in percent germination at 0–0.5 Mol l ⁻¹ NaCl concentrations and significant increases in root length, shoot length, vigor index, and the fresh weight of <i>S. brachiata</i>	Jha et al. (2012)
<i>Bacillus</i> , <i>Pseudomonas</i> , <i>Klebsiella</i> , <i>Serratia</i> , <i>Arthrobacter</i> , <i>Streptomyces</i> , <i>Isoptericola</i> , and <i>Microbacterium</i>	<i>Limonium sinense</i>	N ₂ fixation, IAA production, phosphate solubilization, and ACC deaminase activity	Significant increase in plant root length, shoot length, leaf number, and leaf area as compared to the non-inoculated control	Qin et al. (2014)
<i>Klebsiella</i> , <i>Pseudomonas</i> , <i>Agrobacterium</i> , and <i>Ochrobactrum</i>	<i>Arthrocnemum indicum</i>	N ₂ fixation, IAA production, phosphate solubilization, ACC deaminase activity, and HCN production	A significant increase in total N content (up to 76%), maintained ion homeostasis, accumulated less ROS, and enhanced plant growth compared to non-inoculated seedlings	Sharma et al. (2016)

(continued)

Table 1.1 (continued)

Halotolerant bacteria associated with halophytes				
Halotolerant bacteria	Host halophyte	PGP activity	Plant response	References
<i>Corynebacterium</i>	<i>Sesuvium portulacastrum</i>	–	–	Anburaj et al. (2012)
<i>Serratia marcescens</i> and <i>B. cereus</i>	<i>Aster tripolium</i>	IAA production, N ₂ fixation, siderophore production, and ACC deaminase activity	–	Szymańska et al. (2016)
<i>Chromohalobacter</i> , <i>Marinococcus</i> , <i>Halobacillus</i> , <i>Nesterenkonia</i> , <i>Halomonas</i> , <i>Oceanobacillus</i> , and <i>Virgibacillus</i>	<i>Salicornia strobilacea</i>	IAA, N ₂ fixation, phosphate solubilization, and ACC deaminase activity	–	Mapelli et al. (2013)
Halotolerant bacteria associated with rhizospheric soil				
Halotolerant bacteria	Host	PGP activity	Plant response	References
<i>Bacillus amyloliquefaciens</i> RWL-1	<i>Oryza sativa</i>	–	Decrease in abscisic acid (ABA) production with increase in the levels of endogenous salicylic acid was observed	Shahzad et al. (2017)
<i>Streptomyces</i> sp. strain PGPA39	<i>Solanum lycopersicum</i>	ACC deaminase activity and IAA production and phosphate solubilization	Significant increase in plant biomass and chlorophyll content and a reduction in leaf proline content	Palaniyandi et al. (2014)
<i>Acinetobacter</i> spp. and <i>Pseudomonas</i> sp.	Barley and oats	Production of ACC deaminase and IAA	Increase in plant biomass which led to greater salt uptake and thus decrease in soil salinity	Chang et al. (2014)

(continued)

Table 1.1 (continued)

Halotolerant bacteria associated with halophytes				
Halotolerant bacteria	Host halophyte	PGP activity	Plant response	References
<i>Pseudomonas pseudoalcaligenes</i> and <i>Bacillus pumilus</i>	Salt-sensitive rice GJ-17	Reduce lipid peroxidation and superoxide dismutase activity	Reduction in toxicity by ROS by reducing plant cell membrane index, cell caspase-like protease activity, and programmed cell death and hence resulted in increased cell viability	Jha and Subramanian (2014)
<i>Pseudomonas putida</i> , <i>Enterobacter cloacae</i> , <i>Serratia ficaria</i> , and <i>Pseudomonas fluorescens</i>	Wheat	–	Enhanced germination percentage, germination rate, and index and improved the nutrient status of the wheat plants	Nadeem et al. (2013)
<i>Rhizobium</i> and <i>Pseudomonas</i> sp.	<i>Vigna radiata</i>	IAA production and ACC deaminase activity	Dry matter increased up to 1.9-fold and salt tolerance index rose by two-fold	Ahmad et al. (2013)
<i>Brachy bacterium saurashtrense</i> (JG-06), <i>Brevibacterium casei</i> (JG-08), and <i>Haerero halobacter</i> (JG-11)	<i>Arachis hypogaea</i>	–	High K ⁺ /Na ⁺ ratio and higher Ca ²⁺ , phosphorus, and nitrogen content	Shukla et al. (2012)
<i>Raoultella planticola</i> Rs-2	Cotton	ACC deaminase activity	Rs-2 reduced the quantities of ethylene and abscisic acid in cotton seedlings and increased indole acetic acid content in cotton seedlings under salinity stress	Wu et al. (2012)
<i>Pseudomonas pseudoalcaligenes</i> , <i>Bacillus pumilus</i>	<i>Oryza sativa</i>	–	Increased concentration of glycinebetaine (compatible solute)	Jha et al. (2011)

(continued)

Table 1.1 (continued)

Halotolerant bacteria associated with halophytes				
Halotolerant bacteria	Host halophyte	PGP activity	Plant response	References
<i>Rhizobium</i> , <i>Pseudomonas</i>	Maize	–	Decreased electrolyte leakage and increase in proline production, maintenance of relative water content of leaves, and selective uptake of Kion	Bano and Fatima (2009)
<i>Bacillus subtilis</i>	<i>Arabidopsis thaliana</i>	–	Tissue-specific regulation of sodium transporter HKT1	Zhang et al. (2008)
Halotolerant AM fungi				
Halotolerant bacteria	Host	Plant response		References
<i>Funneliformis mosseae</i> , <i>Diversispora versiformis</i>	<i>Chrysanthemum morifolium</i>	Root length, shoot and root dry weight, total dry weight, and shoot and root N concentration were higher in mycorrhizal treated plant		Wang et al. (2017)
<i>Glomus intraradices</i>	<i>Phaseolus vulgaris</i>	Maintains the root hydraulic conductance of the plant		Aroca et al. (2007)
<i>Glomus mosseae</i>	Maize	AM symbiosis raised the concentrations of soluble sugars, reducing sugars, soluble protein, total organic acids, oxalic acid, fumaric acid, acetic acid, malic acid, and citric acid and decreased the concentrations of total free amino acids, proline, formic acid, and succinic acid in maize leaves		Sheng et al. (2011)
<i>Glomus intraradices</i>	Lettuce	Higher relative water content with lower proline content and abscisic acid in the roots		Jahromi et al. (2008)
<i>Glomus mosseae</i>	Maize	Mycorrhizal maize plants had higher dry weight of shoot and root, higher relative chlorophyll content, better water status, higher gas exchange capacity, and higher non-photochemistry efficiency		Sheng et al. (2008)

(continued)

Table 1.1 (continued)

Halotolerant bacteria associated with halophytes				
Halotolerant bacteria	Host halophyte	PGP activity	Plant response	References
<i>Glomus intraradices</i>	Tomato	Mycorrhization alleviated salt-induced reduction of P, Ca, and K uptake. Ca/Na and K/Na ratios were also better in AM plants. Mycorrhization improved the net assimilation rates through both elevating stomatal conductance and protecting photochemical processes of PSII against salinity		Hajiboland et al. (2010)
<i>Claroideoglossum etunicatum</i>	<i>Oryza sativa</i>	AM symbiosis enhanced the actual quantum yield of PSII photochemistry and reduced the quantum yield of non-photochemical quenching in rice plants subjected to salinity		Porcel et al. (2015)
<i>Glomusgeosporum</i> and <i>Glomus intraradices</i>	Tomato	Enhancement of transcript levels of both a tonoplast and a plasmalemma aquaporin gene		Ouziad et al. (2006)
<i>Rhizophagus intraradices</i> , <i>Claroideoglossum etunicatum</i> , and <i>Septoglossum constrictum</i>	Maize	Improved ion homeostasis		Estrada et al. (2013)

acetic acid (IAA), cytokinin, gibberellin, abscisic acid (ABA), etc. which are known to modulate root development and architecture along with signaling in response to stress. Production of IAA or its derivatives is a very common trait in most plant growth-promoting bacteria and is believed to combat salinity stress in plants. *Pseudomonas* strains showing IAA production increased almost 52% of seedling root growth under 100 mM NaCl as compared to control (Egamberdieva et al. 2010, 2011). Egamberdieva et al. (2011) reported that IAA-producing isolates of *Stenotrophomonas* and *Pseudomonas* could alleviate salinity stress in cucumber plants. Zahir et al. (2010) reported IAA production by *Rhizobium phaseoli* improved growth and yield of mung bean under salinity conditions. IAA-producing *Kocuria turfanesensis* strain 2 M4 isolated from rhizosphere of a halotolerant plant showed 17% increase in length and 13% increase in fresh biomass of groundnut plants grown under saline soils (Goswami et al. 2014). Kadmiri et al. (2018) reported that *Pseudomonas* and *Azospirillum* isolates could retain IAA production under hyper-saline conditions and could activate the defense mechanisms in wheat plants under saline conditions. ABA acts as an important internal signaling molecule in plants under adverse environmental conditions like drought, salinity, etc. Microorganisms with the ability to produce ABA can interfere with the plant stress response system

and can confer tolerance to salinity. It was suggested that growth improvement of plants under saline or other stressed conditions upon inoculation with *Azospirillum* sp. might be due to the ability of the bacteria to produce ABA or increase ABA synthesis in plants. Cohen et al. (2008) and Shahzad et al. (2017) reported that inoculation of ABA-producing bacterial endophyte *Bacillus amyloliquefaciens* RWL-1 could enhance the salinity tolerance in rice. Cytokinin is also known to promote plant growth under stress conditions and help plants to survive under saline conditions. Naz et al. (2009), Kang et al. (2012), and Lubovská et al. (2014) reported stimulation of plant growth and proline content under 20 dS/m NaCl condition in soybean inoculated with cytokinin-producing bacteria isolated from weeds growing in highly saline soils. Gibberellins have also been attributed to plant stress response. In comparison to uninoculated plants, gibberellin-producing endophytic *Aspergillus fumigatus*-inoculated plants showed increased growth and photosynthetic rate under salt stress (Khan et al. 2011).

Microorganisms can modulate production of phytohormones in plants which can help in salinity tolerance. *B. subtilis* and *P. fluorescens* were reported to increase IAA and GA₃ while decreasing ABA in radish. This modulation was partially attributed to activation of processes involved in the alleviation of salt stress (Mohamed and Gomaa 2012; Kang et al. 2014). Kang et al. (2014) reported that plant growth-promoting rhizobacterial strains, viz., *Burkholderia cepacia* SE4, *Promicromonospora* sp. SE188, and *Acinetobacter calcoaceticus* SE370, could enhance salicylic acid and GA₄ production which might have reduced the adverse effects of salinity stress in cucumber plants. Khan et al. (2017) also reported regulation of endogenous phytohormones in *Solanum pimpinellifolium* inoculated with plant growth-promoting endophytic bacteria *Sphingomonas* sp. under salinity stress.

1.4.2 Microbial Production of ACC Deaminase in Salinity Tolerance

Under stress conditions including salinity, ethylene level increases in the plant. 1-Aminocyclopropane-1-carboxylate (ACC) is enzymatically converted into ethylene. Many plant growth-promoting bacteria possess an enzyme known as ACC deaminase which can break ACC into ammonia and α -ketobutyrate, thus limiting the synthesis of ethylene which can lead to plant growth inhibition or even death at high concentrations. *Pseudomonas fluorescens* strain TDK1 with ACC deaminase activity could enhance the salinity tolerance in groundnut resulting in higher yield (Saravanakumar and Samiyappan 2007). Jalili et al. (2009) reported that ACC deaminase-producing fluorescent pseudomonads could alleviate the stressful effects on canola. Wu et al. (2012) isolated ACC deaminase-producing *Raoultella planticola* from salinized soil which could increase growth of cotton seedlings by 15.0, 33.7, and 33.3%, respectively. ACC deaminase-producing bacterial isolates belonging to *Bacillus*, *Arthrobacter*, *Isoptericola*, and *Streptomyces* were shown to stimulate the growth of plant under salt stress (Qin et al. 2014). Co-inoculation of ACC deaminase-producing rhizobacterial isolate RHD18 and *Mesorhizobium* resulted in

31.2% increase in dry weight of chickpea under salinity stress (Chaudhary and Sindhu 2017). Win et al. (2018) showed that ACC deaminase-positive endophytic *Pseudomonas* sp. can reduce stress-induced ethylene production in tomato plants under NaCl stress and improve the plant growth. Sarkar et al. (2018) reported that *Burkholderia* sp. MTCC 12259 isolated from coastal rice field can improve the growth of rice through reduction in stress-induced ethylene production.

1.4.3 Microbe-Mediated Improved Osmolyte Accumulation for Salinity Tolerance

Maintenance of internal osmotic balance is key to metabolic activities of plant cells. Production and accumulation of osmolytes in response to salinity is one important strategy employed by plants. Plant-associated microorganisms can also enhance stress tolerance by improving osmolyte accumulation in plants. Zarea et al. (2012) reported higher proline accumulation in wheat upon root colonization with *Azospirillum*. Upadhyay et al. (2012) showed increased proline and total soluble sugar in wheat inoculated with *Arthrobacter* and *Bacillus* significantly contributed to osmotolerance. Kumari et al. (2015) reported that inoculation of *Bacillus* sp. SJ-5 increased proline accumulation in soybean roots which contributed to increased plant tolerance to salinity. Application of *Serratia marcescens* CDP-13 significantly modulated the levels of different osmoprotectants like proline, malondialdehyde, etc. in wheat suggesting their role in adaptation to tolerate salt stressors (Singh and Jha 2016). Yasin et al. (2018) reported that increased accumulation of proline along with upregulation of a number of stress-related genes resulted in improved growth of *Bacillus fortis* strain SSB21-inoculated chili plants under salinity.

1.4.4 Microbe-Mediated Ion Homeostasis for Tolerance to Salinity Stress

Microbes can alter uptake of ions and nutrients through roots mostly via unknown mechanisms. Regulation of Na⁺-K⁺ influx-efflux through microbial inoculation can control the internal ionic balance required for a number of plant metabolic activities. Reduced efflux of potassium ions from roots and higher concentration in shoots and leaves can be helpful in salt stress adaptations in plants. *Azospirillum* inoculation in wheat could restrict root influx of Na⁺ (Ashraf et al. 2004). Inoculating *Arabidopsis* with *B. subtilis* GB03 improved salt tolerance through regulation of the potassium transporter HKT1 (Zhang et al. 2008). Kasotia et al. (2015) also reported reduced Na⁺ levels and increased K⁺ levels in leaves and roots of *Pseudomonas koreensis*-inoculated soybean plants under salt stress. Yun et al. (2018) reported that inoculation of *Piriformospora indica* improved salinity tolerance in maize through improved stomata operation associated with higher rate of K delivery into the shoots by restricting K⁺ efflux from roots and higher K⁺ loading on shoots. Inoculation of AMF in cucumber showed increased tolerance against salinity due to a restriction in

Na uptake by roots and to the homeostasis of nutrient uptake (Hashem et al. 2018). Microorganisms can regulate the expression and activity of plant vacuolar transporters involved in Na⁺ detoxification. Chen et al. (2017) showed that enhanced salt tolerance in maize and arabidopsis was due to spermidine production by *Bacillus amyloliquefaciens* which in turn upregulated vacuolar transporters responsible for sequestration of Na⁺ into vacuoles and expelling Na⁺ from the cell to reduce ion toxicity. Chatterjee et al. (2018) showed that *Brevibacterium linens* RS16 regulated the salt accumulation by modulating vacuolar H⁺ ATPase activity which provided salt tolerance in rice.

1.4.5 Modulation of Antioxidant Production Through Microbial Inoculation

Production of ROS in cells during the salinity stress can damage the membrane lipids and nucleic acids. Plants deploy scavenging enzymes to eliminate the ROS formed in the cells. Microbial inoculation to plants is known to activate these scavenging enzymes so that the ROS can be efficiently removed. Kohler et al. (2009) showed higher induction in antioxidant enzyme activities in *Pseudomonas mendocina*-inoculated lettuce. Inoculation of *Bacillus* sp. on potato showed improved tolerance to salt through induction of ascorbate peroxidase, catalase, and peroxidase enzymes under 200 mM NaCl (Gururani et al. 2013). Islam et al. (2016) reported increased peroxidase, superoxide dismutase, and catalase activity while improving the growth of *Bacillus cereus*-inoculated mung bean under salt stress. Singh and Jha (2016) reported increase in antioxidant enzyme activities in *Stenotrophomonas*-inoculated sorghum under salinity stress. Vimal et al. (2018) showed that rice inoculated with *Curtobacterium albidum* had enhanced antioxidant enzyme activities which was implicated in reduction of salinity stress.

1.4.6 Microorganism-Induced Root Proliferation and Nutritional Enhancement

As roots are the first to sense the salinity in the soil, they are highly affected by salt concentration in the soil solution. Roots selectively absorb ions, and the amount of ions transported to the shoot is significantly different from those available in the soil. Hence, the characteristics of roots in ion and water absorption are critical in salinity tolerance. In general, higher root growth under salinity stress improves all the functions in the roots that response to salinity (An et al. 2003). Plant growth-promoting bacteria are known to produce a number of growth regulators which can influence the root architecture and growth which may in turn be beneficial for salinity tolerance in plants. Nadeem et al. (2013) showed that inoculation of *Enterobacter*, *Pseudomonas*, and *Serratia* to wheat resulted in higher root growth and mitigated the negative impact of salinity. Goswami et al. (2014) also reported increase in root length of *B. licheniformis*-inoculated groundnut plants growing at 50 mM NaCl.

Effect of inoculation of *Bacillus* sp. Inoculation with *Bradyrhizobium japonicum* and salt-tolerant *P. putida* synergistically enhanced salt tolerance in soybean through alteration of root architecture which in turn facilitated N and P acquisition and nodule formation (Egamberdieva et al. 2017). Chili growing under salinity stress was studied by Wang et al. (2018), and it was reported that the bacterial inoculation could alleviate the salinity stress and increase root length by ~146%.

Nutritional status of plants significantly influences their ability to adapt under a range of abiotic stress conditions including salinity. Nutritional imbalance can restrict development and reduce plant growth and yield. Salinity may affect nutrient availability, competitive uptake, transport, and distribution within the plant (Grattan and Grieve 1999). Salinity is known to reduce N and P uptake/accumulation (Feigin 1985; Sharpley et al. 1992). High sodium concentration during salinity can also reduce the availability of potassium. Hence, plant growth-promoting bacteria which can increase the nutrient uptake in plants can be very useful for alleviation of salinity stress. Particularly, the microorganisms which can fix nitrogen, solubilize phosphates, and mobilize potassium have immense potential in this regard. Yadav et al. (2015) implicated the role of P-solubilizing halophilic archaea in P nutrition of vegetations growing on hypersaline soils. Shahid et al. (2018) reported that inoculation of *Planomicrobium* sp. strain MSSA10 enhanced the K, N, and P uptake in pea plants in order to keep optimum chlorophyll and protein levels, which in turn conferred protection to plants from salt-induced lipid peroxidation of membranes.

1.5 Molecular Mechanisms of Microbial Amelioration of Salinity Stress

Microorganisms can produce a number of phytohormone and their derivatives which can elicit several physiological responses to the plants. Microorganisms are known to produce indole acetic acid (IAA), cytokinin, gibberellin, abscisic acid (ABA), etc. which are known to modulate root development and architecture along with signaling in response to salinity. Higher root proliferation due to microbially derived plant hormones also helps in acquisition of nutrients in a better way. Microbes which can mineralize or solubilize essential nutrients in the rhizosphere can also help to reduce the salinity stress through better acquisition of nutrients. Besides microorganisms can also modulate the phytohormone production in plants which in turn contributes to salinity tolerance. ABA acts as an important internal signaling molecule in plants under adverse environmental conditions like drought, salinity, etc. It has been speculated that aquaporins and hydraulic conductance are affected by ABA and microorganisms can influence the levels of ABA (Aroca et al. 2007). Under salinity stress, *Bacillus megaterium*-inoculated maize plants showed increased hydraulic conductance which was correlated with upregulation of two plasma membrane aquaporin protein (ZmPIP) isoforms (Marulanda et al. 2010). Salinity stress tolerance may be also mediated through ABA-independent pathways. A detailed study on salinity tolerance in *Arabidopsis* through inoculation with *Enterobacter* sp. EJ01 revealed less induction of *RD29B* (a gene known to be