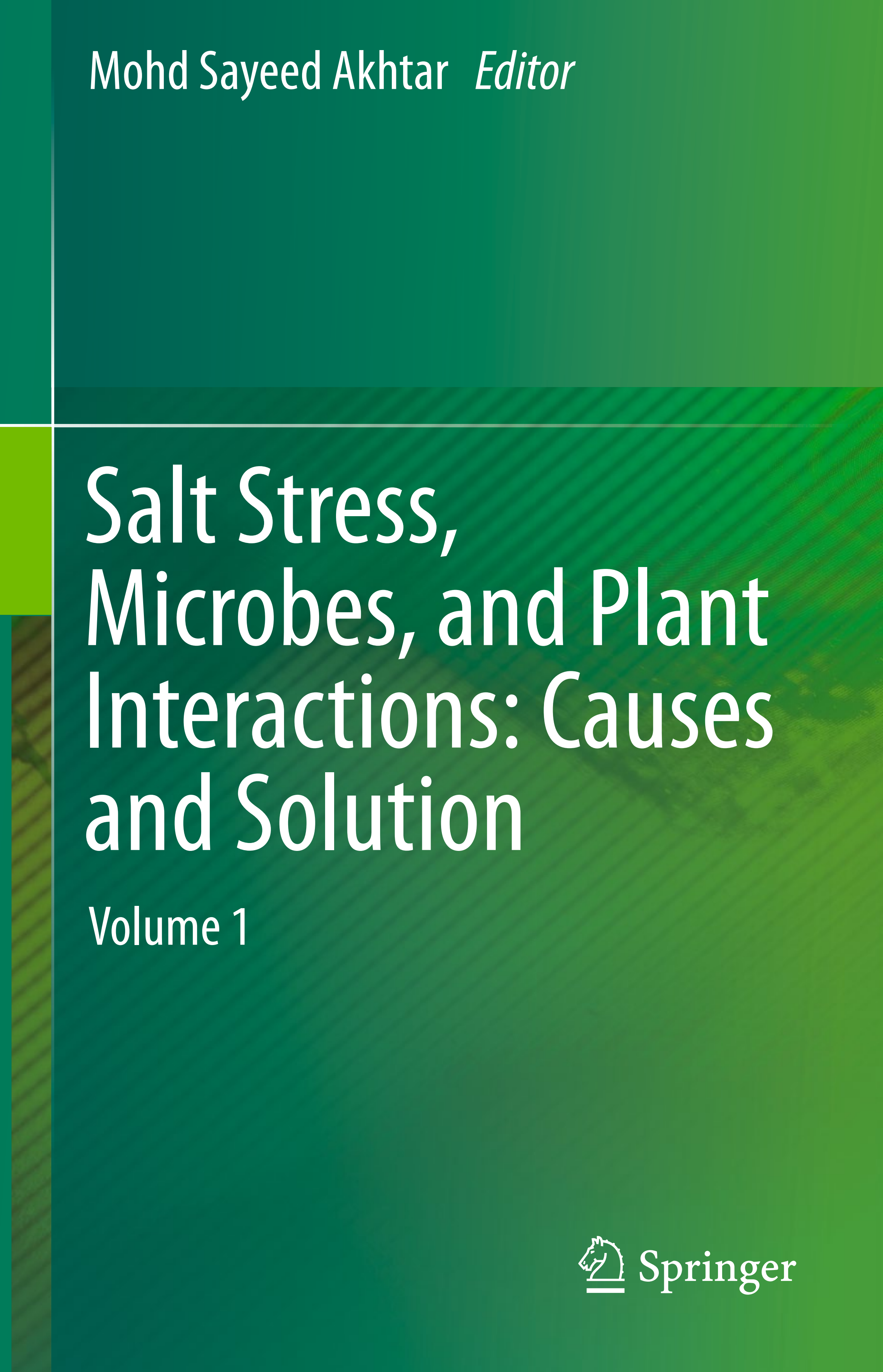

Mohd Sayeed Akhtar *Editor*

Salt Stress, Microbes, and Plant Interactions: Causes and Solution

Volume 1

Springer

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Editor

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This book is dedicated to my grandfather (Dada)

S. Allauddin (1926–1970)

A great visionary, statesman, philosopher, and social reformer of the twentieth century and legendry icon of my life

Foreword

Stressful environments affect not only our soils but also crop productivity. We are in a great need of eco-friendly alternatives for saving our environment. Consequences of the on-going rise in human population, dramatic change in global climate, shrinking agricultural lands, rapid urbanization, and extensive use of agrochemicals are collectively affecting global crop production. In addition to these, climate change is another challenging issue confronting us currently. An excessive and deliberate use of chemicals in our agricultural systems necessitates to look for safe paths. Although we know much about the fact how soil biota can influence physiological responses of plants in particular salt stress, the microbial life in our soils makes it difficult for us to be sure about the importance of particular mechanisms in these interactions in different environments. Any kind of stress serves as the prime factor for limiting agroproductivity. There is an acclimatization under stress conditions originating from the ecological conditions of a species; stress deteriorates the biological mechanisms which growth and productivity endure. Among various types of stresses, abiotic stress is the major cause, limiting global crop productivity; however, the effects on the plant depend on its quantity or intensity; heat, cold, drought, alkaline conditions/salinity, waterlogging, light intensity, and nutrient deficiency are the different types of abiotic stresses. More than three billion ha of drylands are influenced by soil erosion, degradation, and salt stress. Plants possess several defense mechanisms to face such stressful conditions. One of these are the microbes, the supreme natural occupants of different environments with varying physiological and metabolic mechanisms to manage environmental stresses.

The interactions of microbial population with plants are essential for the ecosystem in order to combat with stressful environment. It is becoming more important to characterize and enlighten plant-microbe associations in relation to defense against environmental challenges. Although some beneficial effects of soil biota on the plants found on saline soils is well known, many underlying physiological and molecular mechanisms need to be identified in order to optimize the agronomic applications of soil microorganisms. A better understanding of the different mechanisms involved in plant-microbe and microbe-microbe interactions is a prerequisite for developing new strategies for improving crop yields. These beneficial microorganisms can be used as efficient bioagents in the management of stressed agriculture. Their role in improving nutrient availability to plants seems as an important strategy and related to climate-smart agricultural practices. Majority of the vascular plants form symbiotic associations with mycorrhizal fungi, and many beneficial interactions have been reported. Microbes improve the efficiency of applied fertilizers and manure. Land use changes and the associated loss of beneficial microbial diversity are the major reasons for deterioration of soil fertility and agricultural productivity.

This book *Salt Stress, Microbes and Plant Interactions: Causes and Solution (Volume 1)* to be published by Springer includes 13 chapters. Chapter 1 deals with the challenges regarding agroecosystems. Among these, soil salinity is mentioned as one of the most devastating environmental stresses, which causes major reductions in cultivated land area, crop productivity, and quality. The authors discuss the causes of soil salinity and its impact on crop production due to increasing farming costs under saline soils. They are focussing on the past and present studies on salinity and its economic impact on agricultural system. Chapter 2 presents an overview on the potentiality of plant growth-promoting rhizobacteria in easing of soil salinity and environmental sustainability. In Chapter 3, the use of plant hormones for the improvement of plant growth and production under salt stress has been presented with data from Pakistan. It summarizes the role of hormones such as abscisic acid, cytokinins, gibberellic acid, brassinosteroids, salicylic acid, and jasmonates for improving plant's tolerance and productivity under saline conditions. Chapter 4 deals with the plant growth regulators and salt stress: mechanism of tolerance trade-off with studies from India. The authors are pointing out that in order to improve salt stress tolerance, some sustainable strategies should be chalked out which on one hand engineer salt tolerance and on the other side improve growth, photosynthesis, and yield of plants. They are highlighting the role of PGRs for engineering tolerance against salt stress in various crop plants, together with underlying mechanisms by which plants perceive signals of stress which trigger signal transduction cascades. Chapter 5 focuses on the impact of plant-microbe interactions on plant metabolism under saline environment and also on the involved mechanisms. In Chapter 6, Indian authors entail the plant survival and tolerance under high salinity and also highlighted the primary and secondary cell wall sensing mechanism during salinity stress. However, Chapter 7 presents the results related to the field application of rhizobial inoculants in acidic soils with a case study from Ethiopia. It reviews the field application of faba bean rhizobial inoculants in acidic soils as a promising potential input in organic farming system, highlighting the physiological and molecular events involved in the response and tolerance to soil acidity in legumes, rhizobia, and *Rhizobium*–legume symbiosis. Chapter 8 by Indian investigators discusses the knowledge of heavy metal toxicity, and its remediation using microbes, and also highlighted the utilization of soil microbes for combating the heavy metal stress in plants, while Chapter 9 significantly articulates the use of nanoparticles in alleviating salt stress. Chapter 10 deals with the interaction of soil, plant, and microbes in improving salt stress conditions. However, Chap. 11 emphasizes the mitigation of salinity stresses in the plants through mycorrhizal association. Chapter 12 is titled as "Halophilic Microbe Interactions with Plants to Mitigate Salt Stress" with case study from India. It enlightens the facts related to the use of halophilic plant growth-promoting microbial inoculants in the form of bio-formulations which have future application for the rehabilitation and bioremediation of saline degraded lands, while salinity imbalance and soil nutritional and microbial status on the plant health are summarized in Chap. 13. This volume includes detailed knowledge on salt stress, plant, and microbe interactions with a stress on agronomic, molecular, and ecological approaches. It will open the way for new discussions and efforts to the use of various tools for the improvement of crops under such conditions. I personally congratulate Dr. Mohd Sayeed Akhtar for their noble academic effort in bringing out this volume

Professor (Emer.) of Ecology and Environmental Sciences Münir Öztürk
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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 mechanisms, ion transport, and compartmentalization of injurious ions. To overcome this problem, exploitation of genetic variation; 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: Causes and Solution (Volume 1) incorporates both theoretical and practical aspects and may serve as baseline information at physiological, ecological, biochemical, environmental, and molecular levels for future research through which significant developments can be expected. I hope that this book is helpful for the 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 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 commitment. I am also thankful to Professor Munir Ozturk for his suggestion and writing the foreword for this volume. Moreover, I am thankful to my beloved wife, Mrs. Shagufta Bano, and lovely sons, Mohd. Rafaan 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 Raagaipriya Chandrasekaran, for their generous cooperation at every stage of the publication.

Shahjahanpur, Uttar Pradesh, India 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: Causes and Solution (Volume 1),* along with the forthcoming *Salt Stress, Microbes and Plant Interactions: Mechanisms and Molecular Approaches (Volume 2)*, provides a detail account on the physiological, ecological, biochemical, environmental, and molecular levels for this multi-tropic interaction. Specifically, these two titles 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.

Contents

About the Editor

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 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.

1 Global Concern for Salinity on Various Agro-Ecosystems

Ghulam Mustafa, Mohd Sayeed Akhtar,
and Rabia Abdullah

Abstract

Twenty-first century is marked by many challenges regarding agro-ecosystems, such as environmental pollutions, scarcity of water, and increased salinization of soil and water. Population bomb (increasing human population) and reduction in land available for cultivation are two threats to agricultural sustainability. In this situation, demand for cultivable land increases. However, environmental degradation factors such as erratic rainfall, extreme temperatures, drought and floods, high winds, and soil salinity have affected the production and cultivation of agricultural crops. Among these, soil salinity is one of the most devastating environmental stresses, which causes major reductions in cultivated land areas, crop productivity, and quality. Soil salinity further impacts the general public, particularly farmers, through its effect on agriculture. Therefore, it is necessary to find the causes of soil salinity and its impact (economic and environmental) on crop production in saline soils given the increasing farming costs. Thus, the main focus of the present chapter is to provide an overview of the past and present studies on salinity and its economic impact on the agricultural system.

Keywords

Agro-ecosystems · Economic analysis · Environmental impact · Salinization · Salt stress

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1.1 Introduction

Soil salinity is described as any collection of soluble salts that may be injurious to plants (Machado and Serralheiro 2017). It is the chief restrictive factor that threatens the capability of agricultural crops to meet the demands of the increasing human population. Saline soil contains the salt such as sulfate and chloride of Calcium (Ca), Magnesium (Mg), Sodium (Na), and Potassium (K) (Zaman et al. 2002). Salinity is of major concern in moist areas, and it happens certainly only in coastal areas, depending on sea water imposition or flooding. Moreover, exhaustive fertilization adds insult to injury and causes flooded lands more saline. Additional problems of salinity arise due to increase in supplemented irrigation in humid areas in barren and semiarid regions. For plants, it becomes problematic to extract water from the soil due to the high concentration of soluble salt. Higher level of salt concentrations can be formed due to poor irrigation system, soil drainage, and high level of salt concentrations in irrigation water and unnecessary utilization of manure or dung as fertilizer. Using high salt-concentrated water can affect mostly irrigated areas (salinization). According to an estimate, about 831 million ha of land is affected by salt, which consists of ~7% of the total land in the whole world (FAO 2015).

Management practices regarding soil and waterfor sustainable agriculture production have demoted due to soil salinity. Marginal gains from such management practices also reduce due to saline soil. One of the major factors restricting the production of major crops in the whole world is impacted soil. For the projected population till 2050, a substantial amount of (50%), wheat, rice, and maize is needed to satisfy food demand. The pressure of sustaining the increasing world population has become necessary through soil and plant productivity research. Although resisting salinization, soil pollution and desertification are the major hurdle for sustainablity world population. Under this situation, appropriate biotechnology is expected, which not only expands the productivity of crops but also enhances health of soil via connections of plant roots and soil micro-organisms. Thus, the main focus of the present chapter is to provide an overview of the past and present studies on salinity and its economic impact on agricultural systems.

1.2 Human Population Growth and Agriculture Challenges in the Twenty-First Century

Thomas Malthus (1806) introduced the issue on food security and proposed the hypothesis that increasing global population will ultimately impede the Earth's ability to feed it. "The power of population is indefinitely greater than the power in the earth to produce subsistence for man" (Malthus 1806). This Malthus theory was expanded by Ehrlich, declaring that humans would fail against the battle of hunger. Regardless of Ehrlich's assumptions, it is identified that some social changes have already been appearing that reveal that in some populations, the process of growth is slowing. For example, in most developed nations, the Green Revolution has had greater effect than predicted, and productivity rates have fallen to less than replacement levels (Ehrlich and Ehrlich 2009). The most important challenge that agriculture is facing now is the ability to produce enough amount of food to meet the demands of the growing global population. The world population is likely to reach 10 billion by 2059, which means greater demand for agricultural production. Presently, worldwide population growth is decelerating, but after 2050 and in the succeeding era, population will tend to grow in some areas. With the increase in population, people prefer to live in urban areas than in rural areas. This trend of urbanization has implications on the food system. Scenarios of population growth in different decades is estimated by the United Nations Population Division in three contexts: high, medium, and low alternates. Anticipated variations in these alternates are shown in Fig. 1.1, in which medium alternate is used as reference.

Figure 1.1 shows that nearly in the past years, the annual growth rate of the global population is decreasing. In the peak period of 1960, world population growth rate was 2% per annum with total fertility rate (TFR) of 4.5. In 2015, with the decrease in TFR to 2.5, the growth rate of the global population also decreased 1.2% annually. Meanwhile, absolute annual increments have been increased regardless of the fact that population growth is decreasing. Recently, absolute annual increment is lower than 80 million people.

Absolute increments in medium alternative tend to decrease gradually 55 million people in 2050 and by the end of the century 15 million reductions would be there per year. These increments, cumulatively, will leave 9.73 billion of world population in 2050 and 11.2 billion in 2100 (Fig. 1.2). Among low-income, middle-income and high-income regions these universal tendencies are substantially different. In middle- and low-income countries, population growth will decrease in the medium and even long run, whereas over the period up to 2040, high-income countries will reach their maximum population size. Even in low-income countries, population growth rates will also significantly differ. Figure 1.3 illustrates that in between 2050 and 2060, the higher-populated continent, Asia, would attain its population peak. In East Asia, sustained and increasing growth rates are expected, but after 2040, population growth will decline. After 2070 South Asia will reach at its population peak and it will suffer after that peak point. Population growth is likely slow in Latin America, and this area will not attain its maximum population size during the estimated period up to 2060. After 2080, sudden and more robust progress is predictable for North and East Africa areas. It is estimated that global population growth will continuously increase to 11.2 billion people by 2100.

For many eras, people had lived chiefly in rural places. Thirty-five years ago, more than 60% of the population lived in rural areas. Thereafter, this rural trend changed tremendously, and now more than half (54%) of the world's population is living in urban areas. For the period up to 2050, more than two thirds of the people might be living in urban zones (UN 2015). Agricultural changes due to technical progress and labor-saving techniques aided to meet the food demands of urbanization. But at the same time, urbanization has a great impact on agriculture, nutrition and food.

In developing countries, urbanization is surging in similar numbers. Urbanization has great implications on the food system. It is projected that in

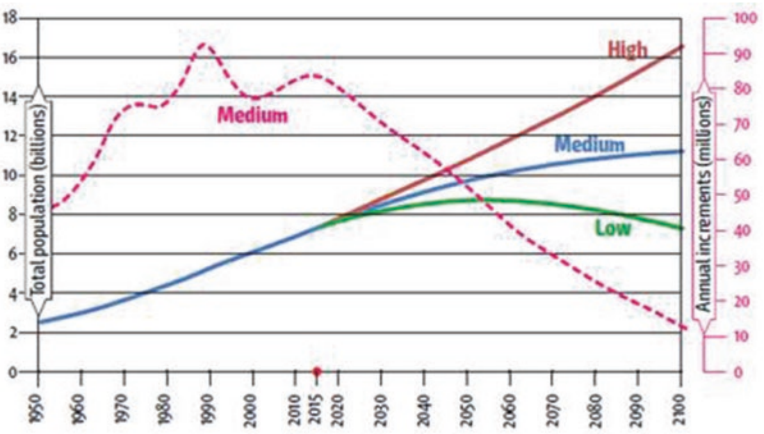

Fig. 1.1 Global population growth up to 2100, by variant

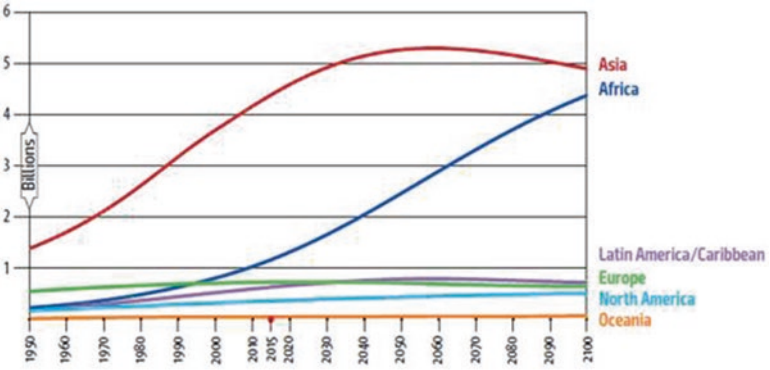

Fig. 1.2 Population growth up to 2100, by region (Medium variant)

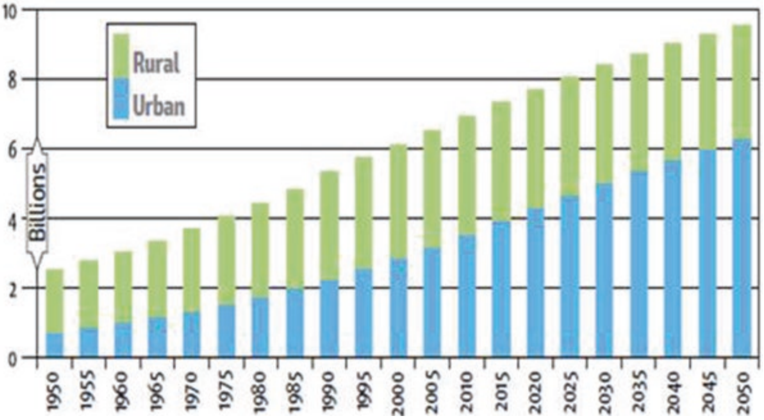

Fig. 1.3 Growth in global urban and rural population up to 2050

rural areas, people would get 60% of their food from their own produce, and the rest they would purchase from the market. However, people in rural areas now purchase 90% of their food from the market. Thus, when one person would migrate from a rural area to an urban one, a twofold increase in food supply will be required. Now the question is where this food will come from in order to meet the demand of the people. Trade expansion would not be the exact measure, seeing the trend in the last 50 years. In late 1960s, the production of global grains more than doubled, so the trade for grains also doubled. Therefore, the traded share of global grain consumption stayed fixed at almost 10%. It means that the majore global grain production (about 90%) would be consumed in the same producing country. If this tendency remains same the countries of high population growth rate would be the drivers to increase food production system. From 2000 to 2030, population will rise in the Tropic of Cancer and Tropic of Capricorn areas and will even undergo speedy population growth. Due to these facts, it is recommended that, in the next 25 years, tropical and subtropical systems of farming be used to produce enough food to fulfill the increasing demand of the population. However, these farming systems in tropical and subtropical areas are highly assorted, difficult, low in productivity, unstable and subjected by small scale poor farmers.

During the Green Revolution, the use of more land for productivity, irrigation, and agricultural chemicals performed a key roles in the evolution of agricultural production. But, now, it is identified that extensive use of lands for more productions put frequently negative impacts on natural resources of agriculture containing irrigated areas' salinization, land degradation, over eradication of ground water, ablation of biodiversity and increase of pest resistance. Agriculture also caused other damages to the environment because of the emission of greenhouse gases, deforestation, and water pollution (FAO 2011a). Figure 1.4 indicates that in the 1990s, at the world level, average growth in the production of rice, wheat, and maize has been only 1% lower than in the 1960s, whereas sugarcane and soybean production remains below 1%. Since the extra quantities of food will be required in this century due to high polpulation growth. This extra food will be produced chiefly by increasing yield rather than expansion of cultivated areas. Ceral productivity growth rate is lower than one percent and this would be a worrying indication if the growth rate will not be increased. Moreover, in low-income and high-income countries, there is a great variation in the yield of crops. In low-income countries, the productivity of rice and wheat is presently about half of that of their counterparts, while productivity of major crops also considerably varies across the areas. More than 50% gaps of potential productivity is estimated in the low-income countries and this gap is largest (76%) in sub Saharan Africa and lower (11%) in East Asia. The farm productivity gaps lead to constraints such as an inadequate adaptation of more productive technologies, lack of market integration in small-scale family farming and gender inequalities (FAO 2011b). In agriculture, gender inequalities are high where females are underpaid (Sen 1999). This is due to the constraints emerged from farm productivity gaps. Thus, the challenge of food productivity is not so simple; it requires the maximum

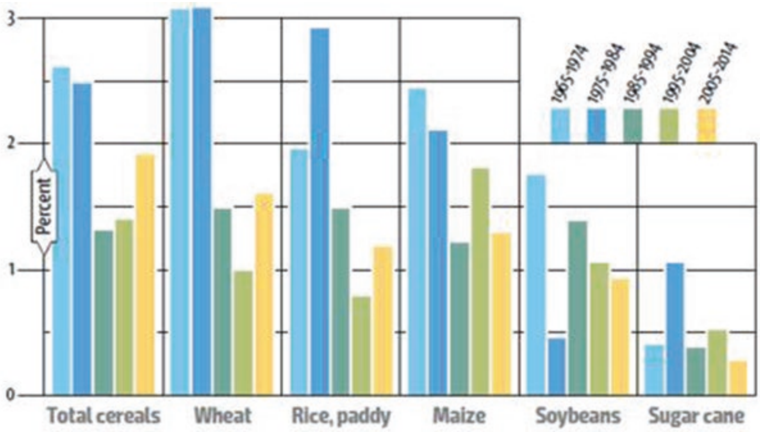

Fig. 1.4 Average annual growth rate for selected crop yields

productivity of complicated and low-producing land in a manner that would not deplete the physical environment and natural resources.

1.3 Global Concern About Soil Salinity

The beginning of the twenty-first century has been marked by global challenges of environmental pollution, water resource scarcity, and augmented salinization of soil and water. There are two main threats for agricultural sustainability: growing human population and lack of land for cultivation (Shahbaz and Ashraf 2013). It has been assessed that globally 33% of irrigated agricultural lands, and 20% of total cultivated land are affected by salinity. Additionally, the rate of salinized areas increases by 10% annually due to numerous reasons, high surface evaporation, weathering of native rocks, including low precipitation, poor cultural practices, and irrigation with saline water. By the year 2050, it has been calculated that more than 50% of the cultivated land would be salinized (Jamil et al. 2011).

Soil salinity would afflict approximately 831 million hectares of land worldwide (Martinez-Beltrán and Manzur 2005), and salinization is expected to affect 50% of all cultivated land by 2050 (Wang et al. 2003). Globally, the degree of salinization has both economic and social implications. Soil salinity not only reduces the agricultural productivity but it also hampers both the global supply of food and agricultural profits. Due to the decline in crop productivity globally, US$12 to 27.3 billion is lost annually (Qadir et al. 2014). According to the World Bank, soil salinization initiated by unsuitable irrigation exercises disturbs about 60 million ha, or 24%, of all irrigated land globally. In Africa, 50% of irrigated land is threatened due to salinization (Ceuppens and Wopereis 1999). Cumulative soil salinization is rising also in China, Central Asia, India, and Pakistan (Wichelns 1999). Practically, 35% of agricultural land undergoes salinity in Egypt (Kim and Sultan 2002, Kotb et al.

2000). The first stage of environmental destruction is soil salinization. This salinization is caused by lake and river salinization. For instance, the deviation of the Syr Darya and Amu Darya rivers not only caused momentous dehydration of the Aral Sea but also led to salinization of related agricultural land (Weinthal 2002). Soil salinization is the most critical environmental problem in Australia, initiating a dramatic change in the industry, landscape, and the future of farmland in the continent (Dehaan and Taylor 2002, Vengosh 2003). Salinity is considered a more severe problem. It occurred in Euphrates and Tigris in 4000 BC and has been a 6000-year-old problem and still affects the people of Mesopotamia.

Salinity is the most severe problem in the agricultural sector. It affects agricultural crops, and as a result, crop productivity is very low and economic development and economic growth are also low. Salinity impacts infrastructure, water supplies, the social system, and the stability of the communities. In cases of salinity, water is not given properly to plants, as needed for irrigation. That's why salt is not mixed in land. As a result, salt lives above the area of the land. Due to this, salt gathers in the zone of roots. Consequently, the land cannot work properly, and production efficiency becomes low; therefore, the land is not able to produce anything. Soil salinity is among the most important concerns globally. It turns productive land into unproductive land and also affects plant growth and agricultural production. The amount of arable land all over the world is 1.5 billion ha; because of high salinity, 77 million ha is now unfitting for crop growth. In many parts of the world, the amount of land covered by saline soil is increasing, especially those areas where temperatures and rates of evaporation are high and rain is low under arid and semiarid conditions. More than 7% of the total land on Earth is arid and semiarid. Some specific regional cases are tabulated in Table 1.1.

In different seaside districts in Bangladesh, water and soil salinity is a collective problem. Significant losses of ecosystem functions and services are as a result of soil salinity such as soil degradation, deforestation, demolition of farmhouse vegetation and loss of seaside vegetation. In the Salinity Survey Report 2010 of Bangladesh, about 2.5 million acres of cultivated land is affected by soil salinity to varying degrees, accounting for 70% of the total cultivable area (SRDI 2010). In Bangladesh, 2.5 million acres of land that is cultivated is affected by soil salinity,

Table 1.1 Global distribution of land impacted by soil salinity. (FAO 2015)

Region	Extent of salinization (million hectares)
Middle East	91.5
Asia	193.8
Africa	122.9
North America	6.2
Central and South America	71.5
Europe	6.7
Australia	17.6

which is about 70% of the total cultivable area. California has soils that naturally hold high levels of salt, like many arid and semiarid regions. Salinity has started to influence on fertile agricultural land is a very real issue for the people. In reaction to their understanding of the changes related to the salinity trend, people have been found to exploit the seasonal changeability of salinity rules in their local area. For instance, people living next to the Pasur River have occupied another strategy by gaining access to agricultural land in the Dacope sub-district, right across the Pasur, where land is appropriate for rice and winter crop cultivation. Increase in soil salinity has affected the production of rice. Rice is temperately sensitive to soil salinity. This is the case of Bangladesh, a developing country; USA is also not an exception where California has soils that naturally hold high levels of salt, like many arid and semiarid regions.

1.4 Causes of Soil Salinity

Salinity negatively affects plant growth and lessens yield. It damages infrastructure like roads, pipes, cables, and bricks. It diminishes water quality for human usage. It severely damages crops too. Salinity also causes land degradation problems. Agricultural losses due to salinity are difficult to assess, but it is estimated and expected to increase with time. Secondary agricultural land salinization is widespread in arid and semiarid environments where crop production requires irrigation schemes. Whereas the world's population continues to rise, the total land area under irrigation appears to have leveled off. There is a need for increased food production, and this can be met by increasing yield per land area. To reach this goal, genetic engineering of crops for enhanced salt tolerance will be a very important task. In dry regions where freshwater becomes a scarce commodity, irrigation of moderately salt tolerant crops is feasible. Salinity is one of the most important environmental factors limiting the productivity of agricultural crops, and there are many reasons for soil salinity, as given below.

1.4.1 Natural or Primary Salinity

Primary soil salinity is also known as naturally occurring soil salinity. It has natural causes like the accumulation of salt for a long period of time, mostly in arid and semiarid areas. It arises due to two main natural processes. Firstly, it is caused by weathering of parent rocks, through which soil is made. Weathering processes rundown rocks and discharge soluble salts of various types. These rocks contain salt such as chlorides of sodium (Na) calcium (Ca) and magnesium (Mg). They also contain sulfates and carbonates to some extent. Secondly, primary salinity is caused by the accretion of ocean salt carried by the rain and wind. In low-lying areas along the coast, soils are affected by sea water. Sea water is a source of salts. Oceanic salt or cyclic salt transferred in wind due to heat of sun (water cycle) and accumulated

Table 1.2 Magnitude of salt affected soils

Regions	Sodic soils	%	Saline soils	%	Total area
Europe	72.7	3.6	6.7	0.3	2010.8
Asia and Pacific Australia	248.6	8.0	195.1	6.3	3107.2
North America	14.5	0.8	4.6	0.2	1923.7
Africa	33.5	1.8	38.7	2.0	1899.1
Latin America	50.9	2.5	60.5	3.0	2038.6
Near East	14.1	0.8	91.5	5.1	1801.9
Total	434.3	3.4	397.1	3.1	12781.3

Adopted from Gnassemi et al. (1995)

by rainfall. Rainwater is composed of 6–50 mg/kg of salt, and as the distance from the coast increases, the intensity of salt reduces.

FAO estimated the total area of saline soil using the FAO/UNESCO soil map of the world (1970–1980). It found that there are 397 million ha salt-affected area and 434 million ha sodic soil (Table 1.2). There is almost 1500 million ha of agricultural dryland, and 32 million ha (2.1%) are salt affected. Meanwhile, there are 230 million ha of irrigated land, and 45 million ha (19.5%) are salt-affected soils, as indicated in Table 1.2.

1.4.2 Secondary/Human Tempted Salinity

Human activities such as land clearing and irrigation are also affecting a major portion of land and making the soil saline. Secondary salinity is the consequence of human actions which transform the soil's hydrologic balance between rainfall or water used for irrigation and water employed by crop transpiration. The detail of secondary soil salinity is given in (Table 1.3). There are two causes of secondary salinity. Firstly, the replacement of persistent vegetation through annual crops and land clearing caused secondary soil salinization. Secondly, the irrigation structures consuming inadequate drainage or by utilizing salt-rich irrigation water lead to secondary soil salinization. In arid or semiarid surroundings, the water utilized by natural vegetation was stable with rainfall before human's activities regarding extensive use of land. This certified that the water tables were well under the surface due to the deep roots of natural vegetation. But, this balance changed with irrigation and clearing of lands so that irrigation water and rainfall delivered extra water than the crops might utilize. This extra water raised the water table and the earlier stored salt organized in the subsoil and carried them up to the root region. Plants utilize water according to their need and depart salt until the soil water converted to saline for additional water taken up by plants. Thus, water table endures to rise and become near to surface. Salt scalds established with the evaporation of water, and leaving salt behind on the ground thus increase soil salinity.

Table 1.3 Global estimate of secondary salinization in the world's irrigated lands

Country	Area of irrigated land that is salt affected		Area irrigated		Total land area cropped (million ha)
	Million ha	%	Million ha	%	
China	6.7	15	45	46	97
India	7.0	17	42	25	169
Soviet Union	3.7	18	21	9	233
United Stated	4.2	23	18	10	190
Pakistan	4.2	26	16	78	21
Iran	1.7	30	6	39	15
Thailand	0.4	10	4	20	20
Egypt	0.9	33	3	100	3
Australia	0.2	9	2	4	47
Argentina	0.6	34	2	5	36
South Africa	0.1	9	1	9	13
Subtotal	29.6	20	159	19	843
World	45.4	20	227	15	1474

Adopted from Gnassemi et al. (1995)

1.4.3 Shortage of Freshwater

Deficiency of freshwater, including rain, rivers, and canals, is one of the chief reasons for soil salinity. For instance, insufficient rainfall is not enough to leach salts and excess sodium ions out of the rhizosphere (the narrow region of soil). Although water is abundant on the Earth's surface, and about 70% of our planet is covered by water, only 2.5% of total water is fresh. For instance, in Southern Punjab and other areas of Pakistan, where underground water is salty, out of the total land surface, almost 10% is covered by various forms of salt-affected soils while 20% of irrigated lands are affected by salinity (Jamil et al. 2011). Lands are being irrigated with tube wells and salty waters due to shortage of freshwater, and this continuous phenomenon creates salt-affected agriculture lands.

1.4.4 Salt Contamination

Through the process of osmosis, water is grabbed up by the fine roots of plants which contain the movement of water from zones of low salt intensity to zones of high salt intensity. The movement of water from the soil to the root is decelerated when salt intensity in the soil is extreme. But when the concentration of salt in the soil becomes excessive than in the inner root cells, then water will be drawn from the root to the soil; the result will be the death of plants. The production of plants is affected by this central mode of salinization. Not only osmotic forces but also toxic levels of chloride and sodium cause soil salinity. Particularly, woody ornamental plants and fruit crops are heavily effected by these elements. Moreover, excess of sodium caused by the high value of pH results in deficiencies of micronutrients.

Salt sensitivity differs in plants. Onions, lettuce, and tomatoes have lower salt acceptance, while halophytes most often occur on beaches, salt marshes, and other saline environments. Soil salinization is a common problem in low rainfall areas, and when coupled with poor drainage and irrigation, it can result in eternal soil fertility loss. Salinity in low rain fall areas is a common aspect in drought-induced humanitarian crises. Soil salinization, as a part of climatic variations, has been yet restricted entirely to tsunamis. That is why FAO is responsive and it employed several humanitarian administrations in Aceh, Indonesia. It may not have formerly confronted the phenomenon and to identify and deal with salt-affected soils due to lack of available information. Providentially, Aceh Province is bestowed with ample rainfall, which is not the case in most areas having soil salinity problems. Most areas have natural soil salinity, whereas in some areas soil salinity is caused by wind that blows nearby oceans and seas. Additionally, it has been noticed in European countries that there is upsurge in sea levels, because of which flood occurs, which in turn causes soil salinity. In most places in the world, soil salinity occurs naturally, while in some parts it is caused by the winds that blow near seas and oceans.

1.4.5 Soil Degradation

Soil degradation is another main cause of soil salinity because of the massive use of chemicals, fertilizers, and other related tools. It includes water erosion, fertility decline, wind erosion salinization, and water logging. Saline and/or sodic soil is caused by four separate conditions: (i) high salt in the parent material and low rainfall (low leaching), (ii) high rainfall with poor internal drainage, (iii) high water table that carries salt to the soil surface, and (iv) high amount of salt being applied through chemicals, manure, and poor quality irrigation water.

1.5 Impact of Soil Salinity

Generally, soil salinity affects the supply chains of agricultural products. However, their negative impact on the various ecosystems can be categorized as follows.

1.5.1 Direct Effect

In the short run, salinity impacts crops, which ultimately impact the food security and well-being of farmers because of decrease in crop production. Salt-affected areas provide less production in case of moderate soil-affected areas and sometimes no production at all in case of extreme salinity.

1.5.2 Indirect Effect

In the long run, soil salinity degrades the value of the land because of its effect on crops; hence, the long-term impact of soil salinity may result in lower land valuations on these areas. This is due to the fact that when underground water becomes saline, the lands become unsuitable for residing and agriculture purposes. This phenomenon lessens the economic value of the land.

1.5.3 Impact of Salinity on Agriculture

Agricultural crops demonstrate different reactions under salt pressure. Due to salinity, not only the production of agricultural crops declines, but the ecological balance of the area and the physicochemical properties of the soil are also affected. Low agricultural productivity, soil erosion, and low economic returns are the consequences of salinity (Hu and Schmidhalter 2002). Impacts of salinity are the consequences of composite contacts, such as physiological, morphological and biochemical procedures containing water and nutrient uptake, seed germination and plant growth (Singh and Chatrath 2001, Akbarimoghaddam et al. 2011). Salinity disturbs virtually all attributes of plant growth, including vegetative growth, germination, and reproductive development. Soil salinity executes osmotic stress, oxidative stress nutrients (N, Ca, K, P, Fe, and Zn) deficiency, and ion toxicity in plants. This results in restriction of water uptake from the soil and may cause death of plants. Soil environmental factors are the main factors that limit plant growth and the yielding of crops. Mineral toxicities, pH, temperature, structure, salinity, nutrients, water, and soil can all interact to limit plant growth. In saline soils, although pH (<8.5) and ESP (<15%) are not high, CEC is >4 mmhos/cm, and an excess of soluble salt in the subsoil restricts water uptake by crops. There are nutrient deficiencies (either roots are unable to access nutrients or there is lack of these nutrients) in the case of alkalinity. The best way to understand these limitations is to consider them in terms of the interacting factors that directly influence crop growth (OMNI ENVIRO 2018).

Soil salinity substantially lessens the phosphorus (P) uptake of plants since phosphate ions trigger Ca ions (Bano and Fatima 2009). Plants are affected by elements such as chlorine, sodium, and boron because these have distinctive noxious impact on plants. Unnecessary accretion of sodium in cell walls can swiftly lead to osmotic stress and cell death (Munns 2002). If the soil comprises plenty of the toxic components, then plants respond to essential nutrients may be influenced. Higher levels of salt in the soil can disturb the balance of nutrients in the plant or can intervene with the uptake of some nutrients because many salts are also plant nutrients (Blaylock 1994). The process of photosynthesis also affected by soil salinity via reducing leaf area, lowering chlorophyll II substance, conductance of stomatal and to some extent by decreasing photosystem II productivity (Netondo et al. 2004). Salinity disturbs generative development by dwelling stamen filament elongation and microsporogenesis, enriching death of programed cell in some tissue types, deterioration of fertilized embryos and ovule abortion.

Plant growth is adversely affected by specific ion effects (salt stress), nutritional imbalances, low osmotic potential of soil solution (osmotic stress), or a mishmash of these factors (Ashraf 2004). Altogether, these factors produce unpleasant consequences on plant development and growth at biochemical and physiological levels (Munns and James 2003) and at a molecular level (Tester and Davenport 2003). The majority of cereals and horticulture crops are glycophytes, or are sensitive to the consolidation of dissolved ions in the soil solution. Different malfunctions like ionic, secondary disorders and osmotic are created due to higher salinity at the growth and development phase of the plants (Zhu 2002). Osmotic pressure as a prime activity created by salinity usually reduces soil water potential and causes probable cell dehydration (Ondrasek et al. 2009). In plants, stomata closure arises due to osmotic pressure, so the growth of plants are disturbed. For instance, rice as a worldwide cultivated crop is also affected by salinity. Water table has direct effect on the growth of plants, and salinity raises the water table and causes accumulation of salts in the root zone. Around 45 million ha of irrigated land out of 230 million ha irrigated land is salt affected, which mean that 20% of irrigated land is salt effected. Due to high salt concentration in land, almost 1.5 million ha land is taken out of production every year and is not capable of crop production. Therefore, irrigation water also has effects on the soil. It contains calcium (Ca^{2+}), sodium (Na^+), and magnesium (Mg^{2+}). When water is applied to the soil after irrigation, it is mostly used by crops for production and metabolism, or it evaporates directly from the soil to the air. Calcium and magnesium ions are changed into carbonates due to chemical reactions. Sodium doesn’t react and becomes dominant in the soil. However, the salt is left in the soil. As a result, the concentration of sodium is one or two times greater than the presence of macronutrients in the soil.

In relation to micronutrients, sodium is many times greater in magnitude than micronutrients. The high concentration of sodium ions in soil solution can reduce the nutrient ion activity and reacts with others ion by chemical reaction to form tremendous ratios of Na^+/Ca^{2+} or Na^+/K^+. The external osmotic potential rises in soil due to high concentration of cations and their salts especially NaCl. It also reduces the holding capacity of water and also decreases the invasion of water into the roots. The remaining water is in poor condition and is surrounded by a large number of sodium ions. These highly saline soils can be identified by a white layer of dry salt on the surface of the soil. There are some common and significant economic impact of salinity on a country, the industry, and the life of farmers. These are mentioned below.

1.5.3.1 Low Per-Acre Yield

Salinity causes a decline in the production of cultivated crop/acre and increases production cost. Thus, it may reduce the profitable margins of farmers.

1.5.3.2 Low Quality of Crop and Low Pricing

Land is affected by this problem known as salinity. On one side, crop production is low; on the other side, the quality of the crops is declining. These crops are low in calories and are not of fresh quality and do not meet important nutrients required for food supplies. When the quality of crops is low, they lose their competitiveness in the market. Therefore, the product is sold at a low price, which is another negative sign for farmers in terms of production. Thus, farmers' profit and income are reduced.

1.5.3.3 Decline in Productivity

When cultivable land becomes saline, it hampers productivity of land and reduces yield per acre. The production of land workers on is also reduced. So farmers' revenues also decline, which means less incentive for farmers. In developing countries, this is one of the reasons why yield per acre and yield per worker employed in agriculture are low as compared with those of developed nations.

1.5.3.4 Increase in the Cost of Production

Salinity causes the relative cost of production to increase. Per unit cost is also increased for two reasons. First, production is reduced while the cost is high. Second, to combat salinity, water pumps and chemical treatment are needed, which also bear high costs. So the overall cost of production increases, as compared to a healthy land that is free from salinity.

1.5.3.5 Low Income of Farmers

In lands where salinity is prevalent, production of crops is low, productivity is low, and yield per acre is low. Farmers cannot impose high prices on their crop products in the market because of low quality, so their revenues are low. Their profit margins are reduced because of the high cost of production and low prices because of poor quality and less revenues. The overall income of a farmer facing land salinity problems is quite low. This lowers their standard of living and their ability to buy the necessities of life.

1.5.3.6 Food Shortages

In developing countries, the problem of salinity of land is most common. They are agrarian economies, but they fail to produce crops to meet the needs of their nation. They have to import food supplies from the developed world. This is the dilemma of diseases (salinization) born on their lands due to mismanagement and lack of technology to combat salinity. Such countries always suffer from food shortages.

1.5.3.7 High Cost Involved in Combatting Salinity

When land becomes saline, crop production is reduced. Hence, it becomes necessary to combat this problem. There are many scientific and preventive solutions for this problem, but these methods involve high cost and proper, systematic management. These kinds of measures will add more to the cost of production.

1.5.3.8 Shortage of Raw Material in the Industry

Industries are agro based in most developing countries. Most of the industries buy raw materials from the agriculture sector. If agricultural production is low due to the salinity of land, there will be shortage of raw materials for the industry, and then raw materials become expensive. Thus, it creates problems for the industry as it increases the cost of production. Also, industries lose their international competitiveness.

1.5.3.9 Food Security

Most of the crops are source of crucial minerals for human beings. However, salinity may responsible for mineral shortages in billions of people due to reduction of agricultural crops productivities. Thus, salinity may cause food security in the long-run.

1.5.3.10 Dependence on Other Countries for Food Supplies and Raw Materials

Crops used in the industry as raw materials become short due to salinity. On one side there is shortage of raw materials within the industry, and on the other the price tag for the products is quite high. Thus, the industry would need to import raw materials from other countries to maintain production and supplies. They have to be dependent on other nations. Their production becomes solely dependent on the commercial policies of other countries from where they are importing raw materials. Soil salinity pastes heavy costs on the agricultural system because of reduction of yield, increase in input costs, and lower profitability and land value. The negative impact of soil salinity varies from crop to crop. For instance, some crops are more vulnerable to salinity compared with other crops.

1.5.4 Economic Impact of Soil Salinity

Salinity restricts the growth of plants and causes yield to decrease. It erodes infrastructure like cable, pipes, and bricks. The quality of water for human use diminishes, and crops are drastically affected. It also causes the problem of land degradation. There is a need to increase yield and production in order to cover the needs of the increasing population day by day. To meet this goal, this matter should be dealt with scientifically. Salinity is an environmental problem that leads to the decrease in productivity of major crops and production in agriculture in general. Salinity not only reduces the agricultural yield of most crops but also distresses the environmental equilibrium of the region and soil physicochemical characteristics. Low agricultural production, soil deterioration, and low economic revenue are the consequences of salinity (Hu and Schmidhalter 2002). Efficiency of agricultural crops is restrained due to the rigorous environmental factor that is salinity. Soil salinity is created by high consolidation of salts, and most crops are vulnerable to it. In a year, approximately $12 billion agricultural products are lost owing to salinity, and this is anticipated to rise as soils are further distressed (Gnassemi et al. 1995).

Regardless of the economic cost of production, salinity also has serious effects on water supply, the solidity of communities, infrastructure, and social structure. Plants need water and soluble minerals like salts for their optimal development and growth. So two main elements—water and soil—are necessary for cultivation. Even though most of the Earth consists of water, only a small portion (2.5%) of it is freshwater (Ondrasek et al. 2010); that is, only a small portion may be provisionally used for irrigation purposes. The rest is unsuitable for production processes. However, irrigated crops use approximately 70% of fresh water to produce approximately 36% of worldwide food (Howell 2001). In most of the agricultural regions, particularly in developing nations, water insufficiency is prominent owing to population pressure and environmental conditions. As a result, saline water is used for irrigation processes. Therefore, salt-affected land is increasing, and scarcity of food supply is becoming a bigger concern. Most of the cereals and horticultural crops, which are the source of nutrition for humans and animals, are sensitive to excessive consolidation of salts either mixed in irrigation water or existing in the rhizosphere. Salinity has created a havoc for agricultural production. For example, the recent toxic salt waste and sea disturbance in tsunami-damage region of Maldives spoiled 70% of agricultural soil, ruined 370,000 fruit trees and stirred about 15,000 farm operators, with cost predicted at around $ 6.5 million (FAO 2005). However, with the invention of new technologies in agriculture in the form of breeding and molecular biology, it is suggested that salt acceptance in plants is one of the most effective approaches for food production in the existence of salinity.

Na^+ and Cl^- are two of the most significant ions that stimulate salt pressure in plants. Sodium is not an important but a beneficial component, whereas chlorine is a necessary nutrient (Marschner 1995). However, both elements are deadly if these are in too much concentration form, generating particular disorders and creating considerable damages crops. The impact of soil salinity varies from crop to crop and region to region and even varies with regard to the same crop existing in different regions. As there is no generality regarding the impact of salinity on crops, we presented some case studies for different crops in different regions, although mostly salinity impacts the crops negatively.

According to a pioneering study on the issue, in South Asian countries like Pakistan, Iran, India, Bangladesh, Sri Lanka, Afghanistan, Bhutan, and Nepal, the costs of land degradation are at least US$ 10 billion annually. It is almost 2% of GDP in the region, which is equal to 7% of its agricultural value of output (Shah and Arshad 2012).

Shah and Ashraf (2012) found the economic losses due salinization according to the categories of land degradation such as losses due to fertility decline US$ 1.5 billion; water erosion US$ 0.5 billion; and wind erosion US$ 1.8 billion. Further, they found that overall 140 million ha (e.g., 43% of the area's total agricultural land) is affected due to land degradations such as salinization. Out of this, moderately degraded land is 63 million ha, while 31 million ha of land was strongly degraded. The country affected the worst was Iran, with 94% of its agricultural land degraded, followed by Bangladesh (75%), Pakistan (61%), Sri Lanka (44%), Afghanistan (33%), Nepal (26%), India (25%), and Bhutan (10%). Ripplinger et al. (2016) found that on moderately saline soil (5 mmhos/cm), wheat yields are 80%, soybean yields are 16%, and corn yields are 65% of the relative yield. It means that soybean is highly sensitive to increasing salinity. On the revenue side, they found that the expected wheat revenues fall from $214 to $278 per acre, soybean revenues fall from $276 to $50 per acre, and corn revenues fall from $472 to $305 per acre when soil salinity is 5mmhos/cm. On the other hand, Naifer et al. (2011) found that salinity caused havoc to agriculture of Oman. For instance, they estimated that as the soil salinity increases from low to moderate, the damage goes from US 1604ha^{-1} to US2748 ha^{-1}.

NRCS (2012) found that soil salinity caused severe damage to the agriculture of Upper James River, and the productivity of its agriculture decreased by 30%. Further, the report indicated that soybean productivity decreases to 777 thousand bushels ($7.88 million), corn productivity to 3104 thousand bushels ($13.86 million), winter wheat to 250 thousand bushels ($1.44 million), and spring wheat to 512 thousand bushels ($3.02 million) when salinity increases (EC > 4). Tripathi (2009) found out the impact of soil salinity on yields, employment, and human and animal health. He found out that there is an increase of 20–40% and 15–50% health problems, respectively in human and animals, in the Indo-Gangetic Basin in India. He further found out that the crop yield losses in saline soil for cotton, sugarcane, rice, and wheat on salt-affected lands could be 63%, 48%, 45%, and 40%, respectively. In addition, employment losses could be 50–80 man-days ha^{-1}, along with human and animal health issues. The yield losses due to salinity ranged from 36 to 69% (average 48%) and 20 to 43% (average 32%), respectively in rice and wheat crops, in the Indus Basin in Pakistan. Moreover, a study conducted in the Aral Sea Basin in southern Kazakhstan found that 71–86% farm productivity losses occur in magnesium-affected soils, as compared with soils ameliorated by phosphogypssum in the same area (Vyshpolsky et al. 2008).

1.5.5 Impact of Soil Salinity on Ecosystem

Salts in soil may inhibit the growth of plants. Salt presence in the soil reduces the ability of plants to take water, and this restricts the growth of plants. Also, excess salt enters in plants during the process of transpiration and causes injury to plant cells. It reduces the further growth of plants (Greenway and Munns 1980). Salinity may be due to rising water table and water logging, which inhibits the growth of plants and causes weakness in the roots of plants. It hampers farms production systems that further leads to decrease growth of plants and quality of water. Consequently, lower yields of crop production due to salinity. It affects the health of the soil and reduces productivity. Killing of plants erode the soil and leave the soil bare. It also affects wetlands, where salinity increases over a period of time; degrades land gradually; endangers species in wetlands; and harms biodiversity. It also increases soil acidity. Salinity also affects rivers. Salinity gathers in creeks and degrades water supplies to towns and affects horticulture and agriculture and the ecosystem of rivers. Salinity also affects drinking water. When the source of water becomes saline, expensive and extensive treatment is needed to keep the quality of water at a suitable level so that it may be used by humans. Salinity affects roads, pipes, and buildings. It damages all infrastructure, reduces its life, and increases costs of its maintenance. Salinity also affects sports grounds. It reduces grass on the grounds, and the grounds become bare and useless for playing.

1.6 Conclusions and Future Prospects

To meet the demands of food by the increasing global population, agricultural sustainability is required. Available lands have competing use such as for constructions of road, for residence, for industry and for agriculture. On the other hand, the available agricultural land is shrinking due to salinity, and it is assumed that 50% of land is under threat due to salinity in next 50 years. Thus, salinity is the major reason for low yields in various agricultural crops. Therefore, a wide range of adaptation strategies are required in order to cope with soil salinity issues in the near future.

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Potentiality of Plant Growth-Promoting Rhizobacteria in Easing of Soil Salinity and Environmental Sustainability

2

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Abstract

Salinity is one of the most prominent environmental stress found in the cultivated crops worldwide because many of the crops are susceptible to soil salinization resulting from the accumulation of salts in the soil. Salinity alters the physiology and metabolism of plants by a decrease in the rate of photosynthesis, respiration, protein synthesis, and lipid metabolism that lead to a reduction in yield of many crops. To overcome this problem, plants grown in saline conditions are engineered with plant growth-promoting rhizobacteria (PGPR agriculturally important bacteria) that inhabited in the rhizosphere of the plant. Globally, about 20% of cultivable land, as well as 50% of cropland, is under salinity stress according to the United Nations Environment Programme (UNEP). The beneficial effects of PGPR in alleviating salt stress involve boosting key physiological and biochemical pathways, viz., water and nutrient uptake, photosynthetic machinery, ion homeostasis, regulation of osmotic balance, regulation of redox status, capacity, regulation of endogenous phytohormone level, and availability of volatile organic compounds for plants. Therefore, it is recommended that the application of PGPR is an effective means to combat salinity stress in agricultural fields, thereby enhancing world crop productivity. The main emphasis of the chapter is to evaluate the salinity tolerance mechanisms exhibited by PGPR.

Keywords

Ion homeostasis · Osmotic balance · PGPR · Redox status · Soil salinity

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2.1 Introduction

In the current scenario, the practice of sustainable agriculture is critically important to fulfill the accelerating demands of food for rapidly expanding population (estimated to reach 9.6 billion by the year 2050). Traditional and conventional agricultural methods are not enough to meet future agriculture requirements. However, modern techniques like use of synthetic chemicals, fertilizers, and pesticides also contain most of the chemical pollutants which can cause deterioration of the environment and human health. The cultivation as well as production of agriculturally important crops is severely affected by the different abiotic stresses such as soil salinity, fast winds, extremely high temperatures, floods, and drought. Out of the mentioned stresses, soil salinity is the most catastrophic one, which causes huge crop losses in the form of crop productivity, quality, and cultivated land (Yamaguchi and Blumwald 2005; Shahbaz and Ashraf 2013).

Salinity is one among the most brutal stresses that prevails in the environment and limits the productivity of crops (Flowers 2004; Munns and Tester 2008) because several crops are sensitive to high level of soil salinity. It has been evaluated that soil salinity affects more than 20% of total cultivated and 33% of irrigated agricultural lands around the globe. Furthermore, the salted lands are growing at 10% per annum due to certain reasons including high evaporation from surface, low rainfall, weathering of domestic rocks, and traditional cultural activities. From the soil salinization process, more than 50% of the arable land would be affected by the year 2050 (Jamil et al. 2011). In India, it has been expected that approximately seven million hectares of land is affected by salinity stress in India (Patel et al. 2011). Most of the salinized land occurs in the states of Haryana, Punjab, UP, and Bihar and some parts of Rajasthan which comes under the Indo-Gangetic region of India.

Salt stresses alter the physiology and metabolism of the plant, depending on concentration and exposure period of the stress given, and ultimately resulted in reduced crop production (Munns 2005; Rozema and Flowers 2008; Rahnama et al. 2010; James et al. 2011). Dissolved salts destroy the soil fertility by causing antagonistic effects on growth and plant development (Munns and Tester 2008). Initially, soil salinity causes reduction in plant growth related to osmotic stress and ion toxicity (Rahnama et al. 2010; James et al. 2011).

To achieve the vision of sustainable agriculture, cultivated crops need to be well furnished with salt tolerance, disease resistance, heavy metal tolerance, drought tolerance, and better nutritional status. For the above-mentioned crop characteristics, one of the ecologically important strategies is to utilize soil microbes (algae, bacteria, fungi, etc.) that enhance the ability to absorb nutrients and water utilization efficiency (Armada et al. 2014). Out of the potential soil microbes, bacteria which are called as plant growth-promoting rhizobacteria (PGPR) are the most efficient which may be employed to promote plant growth rate and also to boost plant health status in a way in which environment is not affected (Calvo et al. 2014). For decades, a lot of research has been done on varieties of PGPR (including *Azospirillum*, *Bacillus*, *Enterobacter*, *Klebsiella*, *Pseudomonas*, *Serratia*, *Variovorax*, etc.), and some of them have been exploited commercially (Glick 2012). A widely proven concept in plants which contributes to elevated stress tolerance is the ability of soil microorganisms to engineer signaling of phytohormones and trigger several other mechanisms (Dodd and Perez-Alfocea 2012). The effective PGPR should have a high level of rhizosphere competence, ability to boost plant growth, wide range of action, be ecologically safer, be congenial with other rhizobacteria, and be tolerant to oxidizing agents, heat, and ultraviolet radiation (Nakkeeran et al. 2005).

Plants inoculated with beneficial microbes are gaining agronomic attention since they improve cultivation in saline conditions by inducing salt tolerance and hence reestablishing crop productivity (Lugtenberg et al. 2013). Favorable fungi and bacteria can enhance plant growth under stressed environmental conditions which ultimately boost yield in both direct and indirect manner (Dimkpa et al. 2009). Some PGPR may have direct impact on plant growth and development by fixing nitrogen available to plants, soluble phosphate, phytohormones, and iron that has been isolated from bacterial siderophores (Siddiqui et al. 2007; Akhtar and Siddiqui 2009; Hayat et al. 2010). The main emphasis of the chapter is to evaluate the salinity tolerance mechanisms exhibited by PGPR. The information provided in this chapter could be important to those who are serious toward safeguard of environment and practice of sustainable agriculture.

2.2 Soil Salinization and Its Causal Agents

Soil salinization is caused by natural or human activities that increase the concentration of dissolved salts, predominantly sodium chloride in the soil. Primary salinity is caused by natural processes, leading to significant salt accumulation in soil and groundwater over extended periods of time. Sources of primary salinity may be soluble salts released from weathering of rocks and minerals, rainfall that washes these salts downstream, wind-borne salts from oceans and sand dunes that are deposited inland, and influx of seawater followed by subsequent withdrawal (Pitman and Lauchli 2002; Rengasamy 2002). The anthropogenic activities include irrigation of crops with saline waters which leads to dramatic acceleration in soil salinization. The other elements may be inorganic fertilizers and soil amendments including composts, gypsum, and manures. The accumulations of salts in soil enhance sodium (Na^+) present in salt which disturbs the soil structure, degrade soil hydraulic characteristics, increase pH of soil, lower water retention and infiltration, reduce soil aeration leading to soil compaction, and increase erosion and water runoff (Ondrasek et al. 2010). Increased soil salinity decreases the water-absorbing capacity of plants, and consequently large amounts of Na^+ and Cl^- are taken up by roots which negatively influence the plant growth through impaired metabolism and decreased photosynthetic rate (Flowers and Yeo 1995; Maser et al. 2002).

2.3 Impact of Soil Salinity on Plant

Salinity is the cruelest environmental factor reducing plant growth and crop yield because most crop plants are salinity sensitive due to the presence of excessive concentrations of salts in water and soil. Typically, high concentrations of sodium and chloride ions cause the soil salinity. It not only reduces the agricultural productivity of crops but also affects physicochemical properties of the soil. Salinity decreases water potential and causes ion disturbances or imbalance in ion homeostasis. This altered water status leads to the reduction of plant growth and crop yields. Since salt stress involves both ionic and osmotic stress (Hayashi and Murata 1998), reduction of plant growth is directly related to the osmotic potential of soil water or the total amount of soluble salts (Greenway and Munns 1980). It affects most of the developmental processes of the plant such as plant growth, transpiration, photosynthesis, water and minerals transport, protein synthesis, lipid metabolism, and reproduction. Effects of salinity are discussed under separate headings.

2.3.1 Effects of Salinity on Growth and Development

Salinity stress reduces the growth of plants (Takemura et al. 2000). It promotes the synthesis of abscisic acid (ABA) that causes stomata closure upon reaching guard cells. Stomata closure results in decline of oxidative stress and photosynthesis. An instant impact of osmotic stress on growth of the plant is reduction in the expansion rate of leaf surface leading to halting of expansion either directly or indirectly through ABA. Further plant reactions to osmotic stress are reduction in cell growth and development, reduced chlorophyll content, accelerated senescence, and defoliation (Shannon and Grieve 1998). Salinity stress also results in the reduction of fresh and dry weights of roots, stems, and leaves (Chartzoulakis and Klapaki 2000; Hernandez et al. 1995). In *Rhizophora mucronata*, at 50% seawater the plant growth is optimum and reduces with further increases in salinity stress (Aziz and Khan 2001a). In *Salicornia rubra*, optimal growth occurs at 200 mM NaCl and reduces with further increase in NaCl concentration (Aziz and Khan 2001b). The reduction of plant growth is about 80% at high salinity due to the cessation of leaf surface expansion. The rest (20% reduction of plant growth at high salinity) is due to halting of stomatal conductance. Parida et al. (2004) proved in their experiment that in *Bruguiera parviflora*, a salt nonsecretor mangrove, plant growth is found to be optimal at 100 mM NaCl concentration under hydroponic condition, while decline with a further increase in the concentration of NaCl, 500 mM NaCl, was proved to be fatal in this species. On the contrary, a salt secretor mangrove, i.e., *Aegiceras corniculatum*, can tolerate up to 250 mM concentration of NaCl, whereas 300 mM NaCl concentration was found to be fatal (Mishra and Das 2003). High salinity in the soil is accompanied by significant reductions in plant length, number of leaves, shoot weight, root length, and root weight in tomato (Mohammad et al. 1998).

Salinity stress affects nearly all stages of plant growth and development, namely, germination, vegetative phase, and reproductive phase. The adverse impact of salinity is more profound throughout the reproductive phase. It adversely affects the reproductive phase by enhancing programed cell death of some tissue types, abortion of ovule, and senescence of fertilized embryos and preventing microsporogenesis and elongation of stamen filament. Munns and Rawson (1999) experimentally found that in wheat plants a significant reduction in spikelets per spike, delayed spike emergence, and reduced fertility occurred at 100–175 mM NaCl concentration, which results in fewer yields of grains. Salinity halts the cell cycle by inhibiting the activity and expression of cyclins and cyclin-dependent kinases (CDKs) that result in a few number of cells in the meristem, thus limiting plant growth. The activity of CDKs is also reduced by inhibition of post-translation during salinity stress. Recent reports also show that salinity stress has an adverse impact on the plant growth and development, enzyme activity (Seckin et al. 2009), protein synthesis, DNA, RNA, and mitosis (Tabur and Demir 2010; Javid et al. 2011).

2.3.2 Effects of Salinity on Photosynthesis

Soil salinity also has an impact on photosynthesis primarily by a reduction of leaf surface area, chlorophyll and carotenoid contents of leaves, and halting of stomatal conductance. Chlorophyll contents decrease in salt-susceptible plants such as pea (Hamada and El-Enany 1994), *Phaseolus vulgaris* (Seemann and Critchley 1985), tomato (Lapina and Popov 1970), and potato (Abdullah and Ahmad 1990) and increase in salt-tolerant plants such as mustard (Singh et al. 1990), wheat (Kulshreshtha et al. 1987), and pearl millet (Reddy 1986). Under salinity stress, carotenoid contents decreased in black cumin (Hajar et al. 1996) and increased in rice (Misra et al. 1997). Uptake and accumulation of Cl^- inhibit nitrate reductase activity which results in the disruption of photosynthetic function (Xu et al. 2000). The oldest leaves start to develop chlorosis and fall due to prolonged period of salinity stress (Gadallah 1999; Agastian et al. 2000).

At high salt concentrations, decline in the osmotic potential of soil results in decreased water availability and disrupts the transport of nutrients and water to plant roots (Munns and Rawson 1999; Tester and Davenport 2003). Soil salinity causes both osmotic stress and water stress in plants, and the accumulated salt ions have a toxic effect on plants. The loss of water causes a decrease in turgor pressure of leaf due to which stomata closed, and a decrease in stomatal conductance limits photosynthesis rates (Chaves et al. 2009). There is also an ion imbalance due to the excessive absorption of Na^+ and Cl^- along with decreased absorption of other ions such as Mn^{2+}, K^+, and Ca^{2+} (Flowers and Colmer 2008). Ashraf and Harris (2013) state that the photosynthesis mechanism involves various components including photosynthetic pigments and photosystems, the electron transport system, and CO_2 reduction pathways. Any damage at any level caused by salinity stress may reduce the overall photosynthetic capacity of a green plant. Analyzing chlorophyll fluorescence is an easy and popular method used in studies of plant physiology that can give information about the state of the photosystem II (Maxwell and Johnson 2000). At a high salt concentration, a general decrease in the electron transport rate and in the photochemical quenching parameters but increases in non-photochemical quenching parameters have been reported (Ikbal et al. 2014; Acosta-Motos et al. 2015a, b). In a salt-sensitive rice cultivar, salinity was found to decrease electron transport rate, while in a salt-tolerant cultivar, there is only a slight reduction in electron transport rate. However, non-photochemical quenching parameters were found to be somewhat different under NaCl stress, since non-photochemical quenching parameters increased more in the salt-tolerant cultivar than in the salt-sensitive cultivar (Moradi and Ismail 2007). In salt-sensitive plants, salt stress, besides decreasing the electron transport rate and photochemical quenching parameters, also decreases non-photochemical quenching parameters (Lee et al. 2013; Shu et al. 2013).

2.3.3 Effects of Salinity on Water Uptake and Ion Homeostasis

Salinity disturbs plant water relations because of decreased water availability from the soil as a result of decreased osmotic potential triggered by the toxic effects of the Na^+ and Cl^- (Munns 2005). Under normal condition, plant cells have a higher osmotic potential than the soil due to which they are capable to take up water and essential nutrients from the soil solution. The osmotic pressure of plant cells is lower than the soil solution when salinity stress occurs. Because of it, the plant cannot take up enough water from the soil solution (Kader and Lindberg 2010). Therewith, plant cells will have decreased turgor pressure from which its stomata will be closed for water conservation. Stomata closure can lead to the production of reactive oxygen species (ROS) such as peroxides, superoxide, hydroxyl radical, singlet oxygen, and alpha-oxygen. ROS halts cell processes by the damage of proteins, lipids, and nucleic acids (Parida and Das 2005). The osmotic stress induced with high salinity can cease growth of plant as the plant focuses its energy on conserving water and maintaining ionic balance. To return to normal functioning for plants, the plant must facilitate its own detoxification, homeostasis must be reestablished, and damage must be lessened or prevented (Zhu 2001).

Salinity halts the distribution of/disturbs ion homeostasis at the cellular and whole plant levels (Tunçtürk et al. 2011). An increase in uptake of NaCl disrupts the absorption of other nutrient ions resulting in K^+ deficiency. Salinity can increase the concentrations of Na^+, Ca^{2+}, and Cl^- in broad bean and decrease the ratio of K^+/Na^+ (Gadallah 1999). High concentration of K^+ is necessary for proper functions in the cell by activation of enzyme, neutralization of negative charges on proteins, and stabilization of protein synthesis (Pandolfi et al. 2012). Under salinity stress condition, high Na^+ and Cl^- concentrations in *U. fasciata* induced the proline accumulation which results in a decreased concentration of proline dehydrogenase and water-soluble Ca^{2+} (Lee and Liu 1999).

2.3.4 Effects of Salinity on Nutrient Uptake

An increase of Na^+ uptake and decrease of Ca^{2+} and K^+ uptake in leaves cause nutritional imbalances. Under salinity stress, nutrient imbalances affect the availability, transport, and partitioning of nutrients resulting in reduced plant growth. However, salinity may differentially affect the plant's mineral nutrient. Plant growth reduces under saline condition because of specific ion toxicities (e.g., Na^+ and Cl^-) and ionic imbalances acting on biophysical and/or metabolic components of plant growth (Grattan and Grieves 1998). Increased NaCl concentration has been reported to stimulate the increase in Na^+ and Cl^-, as well as the decrease in N, P, K, Mg, and Ca level in *Trachyspermum ammi* (Ashraf and Orooj 2006), fennel (El-Wahab 2006), lemon verbena and peppermint (Tabatabaie and Nazari 2007), *Matricaria recutita* (Baghalian et al. 2008), and *Achillea fragratissima* (El-Aty et al. 2009).

2.4 PGPR-Mediated Mitigation of Salinity in Plants

Salinity is one of the major abiotic factors that limit agricultural productivity (Shukla et al. 2012). Several physiological, biochemical/physiochemical, and metabolic processes are affected by salt stress that retards plant growth. Nutrient disturbances, which affect the accessibility, transport, and partitioning/distribution of nutrients, result in growth retardation during salinity which may be accredited to the competition of Na^+ and Cl^- with mineral ions such as K^+, Ca^{2+}, and NO_3^- (Hu and Schmidhalter 2005). Kloepper et al. (1980) proposed the word PGPR which was coined for fluorescent *Pseudomonas*, a plant growth enhancer that fought against pathogens. Since then, the term has been extended to include all rhizobacteria capable of directly promoting plant growth (Kapulnik et al. 1981; Akhtar et al. 2010). Rhizosphere microbiota contains PGPR which are regarded as indispensable and can promote the growth of the host plant to which they are associated (Bhattacharyya and Jha 2012). PGPR are considered as the important tool in the agriculture sector with instinctive genetic potential (Cook 2000). Researchers since many years ago have been involved in exploiting the PGPR to augment the productivity of the plants. However, in recent years, these beneficial bacteria emerged as key player in mitigation of abiotic stresses in plants. Inoculation of plant growth-promoting rhizobacteria (PGPR) is a relatively cost-efficient and readily utilizable strategy which has been explored as a feasible way to help plants remain healthy when facing environmental stress (Nabti et al. 2015). The PGPR which are dwelling in a stressful environment only can endure stress and stimulate plant growth as these bacteria are well adjusted to such conditions (Lifshitz et al. 1987; Shrivastava and Kumar 2015). A variety of PGPR genera such as *Azospirillum*, *Aeromonas*, *Acetobacter*, *Achromobacter*, *Pseudomonas*, *Bacillus*, *Flavobacterium*, *Chryseobacterium*, *Sinorhizobium*, *Bradyrhizobium*, etc. have been identified for maintaining the growth of various crop plants grown under high salt environment (Etesami and Maheshwari 2018). The plant rhizosphere is enriched with nutrient sources excreted from roots that support the higher growth of the microbial population than the surrounding soil (Lugtenberg and Kamilova 2009). Some of the researches performed in evaluating the role of plant growth-promoting rhizobacteria as salinity stress alleviators have been mentioned in Table 2.1.

The majority of the PGPR colonize the root surface and thrive in spaces between root hairs and rhizodermal layers, whereas some are not physically in contact with

Table 2.1 Plant growth-promoting bacterial induced tolerance to salt stress in different crops

Plant growth-promoting bacteria	Plant	References
Alcaligenes faecalis, *Bacillus pumilus*, *Ochrobactrum* sp.	Rice (*Oryza sativa*)	Bal et al. (2013)
Achromobacter piechaudii	Tomato (*Lycopersicon esculentum*)	Mayak et al. (2004)
Acinetobacter sp. and *Pseudomonas* sp.	Barley (*Hordeum vulgare*) and oats (*Avena sativa*)	Chang et al. (2014)
Aeromonas hydrophila, *B. insolitus*, *Bacillus* sp.	Wheat (*T. aestivum*)	Ashraf et al. (2004)
Agrobacterium rubi, *Burkholderia gladii*, *P. putida*, *B. subtilis*, *B. megaterium*	Radish (*Raphanus sativus*)	Kaymak et al. (2009)
A. brasilense	Chickpeas (*C. arietinum*), faba beans (*Vicia faba*)	Hamaoui et al. (2001)
Azospirillum sp.	Maize (*Zea mays*)	Hamdia et al. (2004)
Azospirillum sp.	Lettuce (*L. sativa*)	Barassi et al. (2006)
Azospirillum sp.	Durum wheat (*T. durum*)	Nabti et al. (2010)
Azospirillum sp.	Wheat (*T. aestivum*)	Zarea et al. (2012)
Azotobacter chroococcum	Maize (*Z. mays*)	Rojas-Tapias et al. (2012)
Bacillus sp., *Ochrobactrum* sp.	Maize (Z. mays)	Principe et al. (2007)
B. subtilis	*Arabidopsis thaliana*	Zhang et al. (2008)
B. Megaterium	Maize (*Zea maize*)	Marulanda et al. (2010)
B. subtilis, *Arthrobacter* sp.	Wheat (*T. aestivum*)	Upadhyay et al. (2012)
Bacillus safensis, *Ochrobactrum pseudogregnonense*	Wheat (*T. aestivum*)	Chakraborty et al. (2013a)
Brachybacterium saurashtrense, *Brevibacterium casei*	Pea nut (*A. hypogaea*)	Shukla et al. (2012)
P. Pseudoalcaligenes	Rice (*O. sativa*)	Diby et al. (2005)
Pseudomonas fluorescens	Black pepper (*Piper nigrum*)	Paul and Sarma (2006)
P. fluorescens	Groundnut (*A. hypogaea*)	Saravanakumar and Samiyappan (2007)
P. syringae, *P. fluorescens*, *Enterobacter aerogenes*	Maize (*Z. mays*)	Nadeem et al. (2007)
P. mendocina	Lettuce (*L. sativa*)	Kohler et al. (2009, 2010)
P. fluorescens, *P. aeruginosa*, *P. stutzeri*	Tomato (*L. esculentum*)	Tank and Saraf (2010)
Pseudomonas sp.	Eggplant (*Solanum melongena*)	Fu et al. (2010)
P. Putida	Cotton (*Gossypium hirsutum*)	Yao et al. (2010)
Pseudomonas pseudoalcaligenes, *Bacillus pumilus*	Rice (*Oryza sativa*)	Jha et al. (2011)
P. extremorientalis, *P. chlororaphis*	Common bean (*Phaseolus vulgaris*)	Egamberdieva (2011)

(continued)

Table 2.1 (continued)

Plant growth-promoting bacteria	Plant	References
P. pseudoalcaligenes, *P. putida*	Chickpea (*Cicer arietinum*)	Patel et al. (2012)
Pseudomonas putida, *Enterobacter cloacae*, *Serratia ficaria, and P. fluorescens*	Wheat (*T. aestivum*)	Nadeem et al. (2013)
Pseudomonas pseudoalcaligenes and Bacillus pumilus	Salt sensitive rice GJ-17	Jha and Subramanian (2014)
Raoultella planticola Rs-2	Cotton *(G. hirsutum*)	Wu et al. (2012)
Rhizobium, *Pseudomonas*	Maize (*Z. mays*)	Bano and Fatima (2009)
Rhizobium sp., *Pseudomonas* sp.	Mung bean (*Vigna radiata*)	Ahmad et al. (2013a)
Streptomyces sp.	Wheat (*T. aestivum*)	Sadeghi et al. (2012)
Streptomyces sp. *strain PGPA39*	"Micro-tom" tomato	Palaniyandi et al. (2014)

the roots (Gray and Smith 2005). Bacteria synthesize specific metabolites that enable them to endure conditions such as high salinity, drought, and severe temperatures (Sandhya and Ali 2015). PGPR are considered as potential players in mitigation of salinity stress in plants (Paul and Lade 2014; Shrivastava and Kumar 2015; Qin et al. 2016). Therefore in salt-affected agricultural lands, the application of halotolerant bacteria would be beneficial in promoting the yields of crop plants. Mechanisms underlining the ability by which bacteria encourage plant growth and avert damage induced by high salt concentration in the soil include phytohormones production such as indoleacetic acid (IAA), gibberellic acid, cytokinins, and ethylene (Spaepen et al. 2009; Mishra et al. 2010); synthesis of enzyme ACC deaminase to diminish the content of ethylene in the roots of developing plants (Dey et al. 2004); synthesis of osmoprotectants (Berg et al. 2013); solubilization of minerals, like phosphorus and potassium (Mishra et al. 2017); and modulation of antioxidant enzymes (Kohler et al. 2009). Salt stress alleviation by PGPR is known in several crop plants. A number of reports have emerged elucidating the key task of PGPR in alleviating salinity stress in various plants such as tomato, groundnut, wheat, rice, red pepper, and radish (Mayak et al. 2004; Saravanakumar and Samiyappan 2007; Shukla et al. 2012; Bal et al. 2013; Upadhyay and Singh 2015; Yildirim et al. 2008).

2.4.1 Role of PGPR in Maintaining Ion Homeostasis

Accumulation of Na^+ and Cl^- ions in plant cell under saline environment is a critical factor accountable for plant senescence and restraining growth. In salt-sensitive plants, elevated Na^+ levels impose toxic effects by upsetting potassium (K^+)-dependent processes, inducing lethal protein conformations, and osmotic stress that results in retardation of plant growth, finally leading to cell death (Chinnusamy et al. 2006; Greenway and Munns 1980). High salt (Na^+) uptake in saline environment competes with the absorption of other mineral ions, particularly K^+, leading to its deficiency. There is enhanced uptake of Na^+ or decline in uptake of Ca^{2+} and K^+ during salinity (Neel et al. 2002), thereby influencing the processes associated with calcium and potassium. Na^+ and Cl^- ions dominated salinity by not only decreasing Ca^{2+} and K^+ availability but also diminishing transport and mobility of Ca^{2+} and K^+ to growing regions of the plant that influences both vegetative and reproductive structures (Grattan and Grieve 1999). Moreover, several researches have revealed that soil containing high levels of Na^+ and Cl^- may slow down nutrient–ion activities and produced acute ratios of Na^+/Ca^{2+} and Na^+/K^+ in the plants, making the plants vulnerable to osmotic and specific ion injury as well as to disorders related to nutritional imbalances that result in poor yield and quality (Grattan and Grieve 1999; Essa 2002; Sivritepe et al. 2003). Therefore, deleterious effects of salinity on growth and yield could be ameliorated by an increase in the level of K^+ and Ca^{2+} in plants during salinity stress (Sivritepe et al. 2003). Potassium causes activation of more than 50 enzymes, which cannot be substituted with Na^+ (Tester and Davenport 2003). Thus it is of prime importance to either compartmentalize or extrude out Na from the cell, thereby leading to salinity tolerance in plants. The numerous physiological and biochemical processes of the plants get influenced due to high salinity which retards plant growth and development and protein synthesis, disturbs nucleic acid metabolism, and decreases photosynthesis and respiration (Zhang and Blumwald 2001; Sairam et al. 2002). Many glycophytes exhibit enhanced tolerance to salinity stress because they have a higher ability for sodium exclusion, maintaining high levels of K^+ /Na^+ ratio (Zhu 2001). Na^+ efflux and K^+ influx are the most imperative mechanisms that plant utilizes for minimizing salinity stress (Fortmeier and Schubert 1995; Shabala and Cuin 2008). One way for plants to keep a low level of Na^+ in the cytosol is to store Na^+ in the vacuole, thus alleviating its toxicity. Na^+ sequestration in the vacuole is a common and important mechanism in plant salt tolerance and is mediated by Na^+/H^+ antiporters (Apse et al. 1999; Mansour and Salama 2004; Rahnama et al. 2011). PGPR stimulate plant growth and tolerance during salinity by contributing in homeostasis of toxic ions. The high-affinity potassium transporter (HKT) gene family (Platten et al. 2006; Horie et al. 2009; Ali et al. 2012) and the salt overly sensitive (SOS) pathway (Shi et al. 2003; Mahajan et al. 2008) both play an important role in regulating Na^+ transport within a plant. Any change in the expression of these genes has been reported to modify the accretion of Na^+ in the shoot eventually mitigating salinity stress. Similarly, PGPR produce exopolysaccharides which form rhizofilm and act as a physical barrier around the roots ultimately leading to enhanced salinity tolerance in plants inoculated with PGPR. Thus modulation in the expression of HKT and SOS and production of exopolysaccharides contribute to ionic homeostasis in plants. Plants under salinity stress must restrict Na^+ uptake and its accumulation in the shoot which is critical for minimizing salt phytotoxicity.

Because of the alike chemical nature of Na^+ and K^+ ions, excess Na^+ ion concentration affects the low-affinity potassium uptake system, thereby rendering K^+ uptake by the roots. Plants increase the uptake of K^+ ions over Na^+ ions by activating high-affinity KC transporters (HKT), and an increase in K^+ concentration relative to

Na^+ in cytoplasm increases salinity tolerance (Rodriguez-Navarro and Rubio 2006). High-affinity K^+ transporters (HKT) cause Na^+ transport in higher plants such as *Arabidopsis*, rice, and wheat (Platten et al. 2006). At physiologically detrimental Na^+ concentrations, yeast expression of wheat HKT1 showed that HKT1 changes from an HKT to a low-affinity Na^+ transporter (Rubio et al. 1995). Na^+ recirculation from shoots to roots has been suggested as a proficient means to guard leaf cells from Na^+ toxicity (Kong-ngern et al. 2012) as leaf vacuolar Na^+ sequestration ability is poor. Movement of Na^+ back to the roots through phloem played a key role in overall tolerance to salt stress in numerous species, such as lupine, clover, sweet pepper, and maize (Tester and Davenport 2003). HKT1 and other HKT proteins are known to work in shoots to recover Na^+ from the xylem, thereby assisting shoot-to-root Na^+ recirculation, as verified in *Arabidopsis* (Berthomieu et al. 2003; Sunarpi et al. 2005; Davenport et al. 2007), rice (Garciadeblás et al. 2003; Ren et al. 2005), and wheat (Huang et al. 2006; James et al. 2006; Byrt et al. 2007). Involvement of HKT transporters in tolerance to salinity has been revealed in both dicot and monocot crops (Hauser and Horie 2010). In *AtHKT1* mutants, hyperaccumulation of Na^+ in shoots and lower Na^+ in roots have been observed reflecting a direct role of *HKT* gene in Na^+ movement across plant tissues.

Beneficial bacteria mediate tissue-specific regulation of HKT1 which provides a new approach for plant protection grown under high soil salinity. Entry of Na^+ in plants is restricted by reduction of root *HKT1*, while stimulation of *HKT1* of shoot assists Na^+ movement from shoot to root, thereby regulating Na^+ equilibrium and conferring salinity tolerance. Parallel with the induction of shoot *HKT1* expression that points out to enhanced shoot-to-root Na^+ recirculation, *Bacillus subtilis* GB03-inoculated plants accumulate fewer Na^+ in shoots compared with control plants (Zhang et al. 2008); meanwhile, the root *HKT1* downregulation promotes declined root as well as whole plant Na^+ content. Therefore, for plant salt tolerance, regulation at tissue level is shown to be vital bestowed by modulation of *HKT1* gene expression. The foremost role of *HKT1* in GB03-induced salinity tolerance is further justified in plants, mutated for *HKT1* gene which illustrated prominent Na^+ content in the shoot than water-treated plants. PGPR emit certain volatiles which have been shown to suppress roots HKT1 expression but upregulate it in shoots, orchestrating lesser Na^+ levels and recirculation of Na^+ in the whole plant in saline environment (Zhang et al. 2008). These results demonstrated that under saline condition bacteria can modulate the expression of an ion high-affinity K^+ transporter (*AtHKT1*) in *Arabidopsis.* There is an increased K^+ concentration in PGPR-inoculated plants, leading to elevated K^+/Na^+ ratio which highlighted their value in tolerance to salinity stress (Kohler et al. 2009; Nadeem et al. 2013; Rojas-Tapias et al. 2012). The reports indicate lower Na^+ concentrations in plants supplied with PGPR under saline conditions (Sharifi et al. 2007). Monocotyledonous plants that are salt tolerant accumulate less Na^+ in their leaves than salt-sensitive counterparts (El-Hendawy et al. 2005), and the K/Na ratio has been considered as a tolerance index. Moreover, in salt-stressed maize inoculated with *Azospirillum*, elevated K^+/Na^+ ratios were found in which selectivity for Na^+, K^+, and Ca^{2+} was altered in favor of the plant (Hamdia et al. 2004). Salinity not only diminishes the availability of

Ca^{2+} and K^+ in plants but also reduces their movement and transport to the growing parts of plants. However, Fu et al. (2010) reported that *Pseudomonas* inoculated eggplants have significantly elevated Ca^{2+} in shoots when compared to the uninoculated eggplant in saline conditions. PGPR *P. putida* is also involved in escalating the absorbability of Mg^{2+} and Ca^{2+} and decreasing the uptake of the Na^+ in cotton (Yao et al. 2010). Thus, PGPR promote growth of plants under salinity by altering the selectivity of sodium, potassium, and calcium ions and maintain a high K^+/Na^+ ratio in plants. A salt-inducible gene known as *TaST* is reported to reduce intracellular Na ion concentration, increase K ion content, and thus also help to retain an elevated K^+/Na^+ ratio in the transgenic *Arabidopsis* (Huang et al. 2012). The role of rhizobacteria in stimulating the *TaST* expression and hence enhancing salt tolerance was confirmed when it was found that expression of *TaST* in roots of wheat was higher in PGPR *Dietzia natronolimnaea* STR1-treated plant (Bharti et al. 2016). Ionic homeostasis in plants is also mediated by a definite signaling pathway (the SOS signaling pathway) which is an important means for the exclusion of Na ions and ion homeostasis control at cellular level (Zhu 2000). The SOS pathway was reported to export Na^+ out of the cell and thus involved in salinity tolerance mechanism in plants.

2.4.2 PGPR Confer Salinity Tolerance by Regulating Redox Status

By limiting photosynthesis salinity decreases carbon uptake during the dark reaction, causing an excess reduction of electron chain of photosynthesis and funneling the photon energy into processes that favor the generation of reactive oxygen species (ROS) (Johnson et al. 2003; Hichem and Mounir 2009). Some of the most vital ROS generated in salinity and drought stress environment include singlet oxygen, superoxide radical (O_2^-), hydroxyl radical (OH), and hydrogen peroxide (H_2O_2) (Zushi and Matsuzoe 2009) that can cause peroxidation of membrane lipids and consequent destruction to proteins, DNA, and lipids (Sgherri et al. 2000; Pompelli et al. 2010; Vardharajula et al. 2011). Overgeneration of ROS is lethal to plants and causes oxidative damage to cellular components, leading to cell death (Noctor and Foyer 1998; Banu et al. 2009, 2010). In order to protect themselves from detrimental effects of ROS, plants possess enzymatic or nonenzymatic antioxidant machinery which works in coordination to counteract toxic ROS. Components of enzymatic system include superoxide dismutase (SOD), catalase (CAT), peroxidase (POD), and glutathione reductase (GR), while nonenzymatic antioxidants consist of ascorbic acid, tocopherol, glutathione, and secondary metabolites; all of these machinery are involved in the removal of ROS to shield the cells against oxidative damage (Abd-Allah et al. 2015). The major ROS-scavenging antioxidant enzymes are catalase (CAT), peroxidase (POX), and ascorbate peroxidase (APX). Improved salinity tolerance is associated with elevated plant antioxidant response which has been shown to be positively associated with decreased oxidative damage (Hasegawa et al. 2000; Mittova et al. 2004; Demiral and Turkan 2005; Hoque et al. 2007a, b, 2008; Banu et al. 2009; El-Shabrawi et al. 2010). Reduction in plant yield has been registered, despite this antioxidant defense system during oxidative stress situation which shows that various stresses (e.g., salinity, drought, etc.) have modified the activities of enzymes as CAT, SOD, peroxidase (POD), and APX in stressed plants (Paul and Lade 2014). Oxidative damage caused by numerous abiotic stresses such as drought, salinity, and heavy metals can be brought under control by bacterial inoculants (Vardharajula et al. 2011). The environmental stress tolerant-PGPR inoculated plants produced by manipulating antioxidant defense systems can survive under oxidative conditions and can be justified by ample evidences available (Wang et al. 2012; Damodaran et al. 2013; Kim et al. 2014; Naveed et al. 2014). PGPR have shown a remarkable enhancement in activities of various plant defense-related enzymes, superoxide dismutase, peroxidase, catalase, polyphenol oxidase, phenylalanine ammonia-lyase, lipoxygenase, and phenolics (Nautiyal et al. 2008; Liang et al. 2011; Chakraborty et al. 2013b). It is now well known that PGPR such as *Bacillus* and *Arthrobacter pascens* exhibit growth encouragement in maize plants exposed to salinity stress and amplification in the activity of ROS-scavenging enzymes such as SOD, POX, CAT, and APX (Ullah and Bano 2015). Furthermore, under saline-stressed conditions, PGPR (e.g., *Enterobacter* spp. and *Bacillus* spp.) inoculated plants (e.g., tomato and gladiolus) exhibited elevated activities of antioxidant enzymes (e.g., APX, SOD, and CAT) than uninoculated plants (Kim et al. 2014). Inoculation of halotolerant bacteria of genera such as *Klebsiella*, *Pseudomonas*, and *Agrobacterium* enhanced growth in saline condition by diminishing ROS production (Sharma et al. 2016). Gururani et al. (2013) reported improvement in plant tolerance to salt stress by two ACC deaminase producers and phosphate solubilizers, *B. pumilus* and *B. firmus* strains, inoculated on potato (*Solanum tuberosum*) by positively influencing photosynthetic activity, higher proline content in tubers, enhancing of mRNA expression, and specific activities of ROS-scavenging enzymes. Similarly, Kim et al. (2014) reported enhancement of reactive oxygen species-scavenging enzyme activities in aerial plant tissue which might contribute in increasing fresh weight, dry weight, and plant height of tomato under salt stress by an ACC deaminase and IAA producer *Enterobacter* sp. strain inoculation. It was also reported that *B. subtilis* (GB03) inoculated white clover with a diminished level of ROS, under salinity stress, leading to a noteworthy decline in membrane lipid peroxidation (Han et al. 2014). *B. subtilis* inoculation in chickpea also stimulated antioxidant machinery leading to the elimination of ROS as reported by Abd-Allah et al. (2018). This elevated activity of H_2O_2 detoxifying enzymes in chickpea such as CAT and POD, in plants supplied with *B. subtilis* (Abd-Allah et al. 2018), modulates growth of the plant by shielding delicate organelles, such as chloroplasts, in which major metabolic processes occur (Han and Lee 2005; Hashem et al. 2016). Moreover, amplification in the activities of defense-related enzymes was also reported in PGPR inoculated wheat by Singh and Jha (2017), respectively. Antioxidant machinery is induced by *A. xylosoxidans* inoculation in *Catharanthus roseus* (Karthikeyan et al. 2012) and in the *Solanum melongena* supplied with *Pseudomonas* sp. DW1 (Fu et al. 2010). The enhancement in activities of enzymes was perhaps due to bacterial inoculation mediated by the synthesis of these enzymes (Wang et al. 2016).

SOD converts superoxide anion that is converted into water and hydrogen peroxide, which is a harmful lipid peroxidant but can be destroyed by CAT and POX antioxidant enzymes. The enzyme POX plays a central role in abolishing the stress generated H_2O_2 and malondialdehyde level, thus rescuing the integrity of the cell membrane. The increase of ROS under high-salinity stress leads to lipid peroxidation in the cell membrane. The main product of membrane lipid peroxidation is malondialdehyde (MDA) when plants are under salt stress, and its level represents the degree of cell membrane damage. Therefore, MDA content can indicate that the plant is under salt stress. Generation of ROS is elevated in plants during soil salinity which enhances lipid peroxidation of membranes and results in the formation of malondialdehyde (MDA) which is the main product of membrane lipid peroxidation (Koca et al. 2006; Yazici et al. 2007). Therefore, amount of MDA in the leaf is vital index to assess tolerance level of plants to salinity (Luna et al. 2000). Thus a reduction in the amount of MDA clearly indicates the mitigation of salt stress in PGPR inoculated plants. *Enterobacter cloacae* strain HSNJ4 enhanced SOD, POD, and CAT activity in canola seedlings, under increased salt stress, thereby reducing MDA content (Li et al. 2017). Inoculation with SBP-9 protects the plants from the salinity stress (Singh and Jha 2017) which is mainly credited to decrease in MDA content. A similar decline in MDA content was registered in plants inoculated with PGPR (Barnawal et al. 2014; Bharti et al. 2014).

Besides stimulating enzymatic antioxidant machinery, inoculation of PGPR with salt-stressed plant also stimulates nonenzymatic components as well. The interactions of *B. subtilis* in chickpea also enhanced the synthesis of nonenzymatic components, i.e., ascorbic acid and reduced glutathione, which are electron donors of antioxidant enzyme-mediated reactions (Abd-Allah et al. 2018). Some of the important ROS-scavenging molecules are ascorbic acid; glutathione and GRs which are the key components of ascorbate-glutathione cycle (Noctor and Foyer 1998). A chain of redox reaction that occurs in ascorbate-glutathione cycle in salt stress leads to the removal of H_2O_2 in chloroplasts, and the cytosol mitigates the effects of oxidative stress on plants. In salt-affected plants, *B. subtilis* supplementation hastens GR activity and elevates ascorbic acid and glutathione contents, which might be due to the protection of the photosynthetic electron transport chain by the maintenance of the $NADP^+/NADPH$ ratio for continuous flow of electrons to molecular oxygen, resulting in diminished generation of superoxide radical (Noctor and Foyer 1998). One of the important means for reducing oxidative damage is the synthesis of polyphenols by plants (Nautiyal et al. 2008; Hichem et al. 2009) which is also a nonenzymatic component for quenching ROS. Polyphenols content is significantly increased in maize leaves due to salinity, and inoculation of *Azotobacter* strains C5 and C9 also enhanced the quantity of polyphenols compared with the respective noninoculated control (Rojas-Tapias et al. 2012). Polyphenols can destroy radical species, thus averting the spread of oxidative chain reactions (Rice-Evans et al. 1997).

2.4.3 PGPR Regulate the Endogenous Phytohormone Level in Salinity-Stressed Plants

It has been well established that phytohormones such as abscisic acid, auxins, brassinosteroids (BRs), gibberellic acid, and cytokinins assist plants to acclimatize to abiotic stresses by generating a wide range of adaptive responses (e.g., mediating growth, development, nutrient distribution, and source/sink transitions) (Bari and Jones 2009; Messing et al. 2010; Ogweno et al. 2008; Peleg and Blumwald 2011). However, one of the negative impacts on plant growth imposed by abiotic stresses is the decline in endogenous contents of these phytohormones. Some bacteria maintains the plant growth in stressful conditions as they can elevate the level of plant hormones by synthesizing and exuding them (Etesami and Maheshwari 2018). Root- associated microbes, belonging to different genera and species including various types such as free-living, symbiotic, or endophytic microbes, can synthesize various types of phytohormones (Sgroy et al. 2009). According to Iqbal and Ashraf (2010) and Alqarawi et al. (2014), the hormonal balance of plants gets perturbed due to salinity; therefore, under salt stress, hormonal homeostasis might be one possible means of phytohormone-induced salinity tolerance in plants. The rhizosphere contains various nutrient-rich metabolites secreted by roots such as amino acids, sugars, fatty acids, and other organic compounds, which attract microbes (Vorholt 2012). In turn, the microbes produce biologically active compounds, including phytohormones (auxins, cytokinins, gibberellins, and ABA), compatible solutes, enzymes, and antifungal compounds. These microbial metabolites can encourage plant growth development, provide resistance to various stresses (abiotic and biotic), perk up nutrient content, and defend plants from various soilborne pathogens (Ruiz-Lozano et al. 2012; Cho et al. 2015; Sorty et al. 2016; Egamberdieva et al. 2017). The beneficial interactions of microbes in plants, their positive impact on plant growth, and their enhancement of stress tolerance in severe environmental conditions have been comprehensively reviewed by Nadeem et al. (2014). Plant growth is modulated by PGPR through their participation in the metabolism of phytohormones, such as auxins, ethylene, gibberellins, abscisic acid, and cytokinins (Turan et al. 2014; Shahzad et al. 2017). Plant growth stimulation and stress tolerance by microbes lie in their ability to synthesize phytohormone in the rhizosphere or root tissue (Etesami et al. 2015). Homeostasis of endogenous growth regulators in plant tissue is influenced by microbial phytohormones (Hashem et al. 2016; Sorty et al. 2016) which play an important role in altering root morphology during salinity-induced stress (Spaepen et al. 2008; Khan et al. 2011).

Plants respond by increasing ethylene levels when exposed to stress conditions that eventually lead to an increase in cell and plant damage (Argueso et al. 2007). A persistently soaring level of ethylene due to stress would affect plant growth and development as it restrains root elongation leading to abnormal root growth (Babalola 2010). Salinity stress also amplifies endogenous ethylene levels that appreciably inhibit both shoot and root enlargement thereby reducing overall growth of plants (Ma et al. 1998; Klassen and Bugbee 2002). Augmented production of ethylene in response to salinity stress has been previously demonstrated in tomato

(O'Donell et al. 1996; Feng and Barker 1992). In many cases blocking the effect of stress ethylene results in mitigation of the stress effect. PGPR employ one such strategy which results in decreased content of ethylene in salt-stressed plants which is the synthesis of enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase that destroys ACC, a precursor to plant ethylene levels (Glick et al. 1994; Jacobson et al. 1994; Glick 1995), thus diminishing the suppressive effect of stress-induced ethylene on root growth. ACC deaminase by adjusting ethylene levels represents one of the important bacterial mechanisms sustaining plant growth in stressed situations, where the ethylene concentration inside the plant might else reach levels inhibitory to plant growth (Glick et al. 1998, 2007; Glick 2014). Thus ethylene-induced inhibition of plant growth was reversed, and these plants generally have well developed roots and shoots and larger biomass accumulation as compared to uninoculated plants. These findings opened a new avenue and showed a possible way for managing plant health and growth under salt stress. There are numerous reports of reduction in ethylene level by inoculation of ACC deaminase-producing bacteria, e.g., *Achromobacter piechaudii* on pepper and tomato plants (Mayak et al. 2004), *A. xylosoxidans* on Madagascar periwinkle (*Catharanthus roseus*) (Karthikeyan et al. 2012), and *B. licheniformis*, *Brevibacterium iodinum*, *and Zhihengliuella alba* on red pepper seedlings (Siddikee et al. 2011), thus conferring salinity tolerance. According to Glick et al. (1994), PGPR strain *P. putida* GR12–2 containing a mutant version of ACC known as AcdS mutant (lacking activity of ACC) lost the ability to encourage root elongation in case of canola.

Besides modulating the amount of ethylene and conferring salinity tolerance in plants, the PGPR stimulatory effect also comes from a manipulation of the complex and balanced network of other plant hormones that directly are involved in growth or stimulation of the root formation. For instance, the biosynthesis of IAA by various PGPR has been demonstrated to enhance root proliferation (Dobbelaere et al. 1999; Khalid et al. 2004). Plant growth-promoting metabolites, for instance, gibberellins and indoleacetic acid, have been shown to be synthesized by *B. amyloliquefaciens* and *B. subtilis* (Turner and Backman 1991; Idriss et al. 2002). Salinity-mediated growth retardation was due to dip in the endogenous level of hormones in the rhizosphere (Zholkevich and Pustovoytova 1993; Jackson 1997), whereas phytohormones released by rhizobacteria positively modulate seedling development (Frankenberger and Arshad 1995; Afzal et al. 2005). The PGPR bind to the surface of roots of growing plants in response to root exudates containing tryptophan and some other small molecules (Kumar et al. 2014). Besides containing tryptophan the roots exudates of some plants contain ACC along with some other molecules like amino acids sugars and organic acids. In rhizosphere, PGPR carry out two important processes. Firstly, PGPR possessing ACC deaminase convert ACC into alpha-ketobutyrate and ammonia (Honma and Shimomura 1978) and secondly they convert tryptophan into auxins. Thus bacterial-produced IAA and endogenous, i.e., plant-produced, IAA synergistically stimulate root proliferation and elongation. Moreover, PGPR IAA can also induce the activity of ACC synthase to manufacture more ACC (Penrose and Glick 2001). ACC acts as a reservoir of nitrogen that enables bacteria to proliferate under any unfavorable condition (Hontzeas et al. 2006), thereby restricting the level of ACC in plants leading to its enhanced growth and bacteria, in turn, and derives nutrition from catabolism of ACC. IAA can also affect the accumulation of ACC deaminase by stimulating the transcription of the plant enzyme ACC synthase (that catalyzes the transformation of S-adenosyl-Met into ACC). The increased amount of ACC will consequently enhance the ethylene content inside the plant, generating stress response. Thus bacteria that synthesize high levels of IAA frequently hinder plant growth. However, this does not essentially occur because there is an inhibition of transcription of auxin response factors as plant ethylene levels rise (Pierik et al. 2006; Prayitno et al. 2006; Glick et al. 2007), thereby restricting the extent of ACC synthase transcription activation by IAA. Moreover, some ACC is secreted by the roots (Bayliss et al. 1997; Penrose and Glick 2001), which is imbibed by the bacteria, and, through the action of ACC deaminase, is converted to ammonia and a-ketobutyrate. Consequently, the amount of ethylene generated by the plant is reduced, thus promoting plant growth.

Several reports point out that IAA producing PGPR that stimulate plant growth such as *S. maltophilia* strain-SBP-9 were found to synthesize phytohormone IAA and cause solubilization of phosphate that prop up the plant growth under the severe condition such as salinity (Egamberdieva 2009; Ramadoss et al. 2013). It is reported that *Azotobacter paspali* exuded indole acetic acid into culture medium which considerably amplified the dry weight of leaves and roots of numerous plants after root treatment (Barea and Brown 1974). Hasnain and Sabri (1996) demonstrated that wheat plant inoculated with *Pseudomonas* sp. encouraged plant growth by minimizing plant uptake of toxic ions and increasing the auxin content. The root length of uninoculated oat seedlings in salt stress was notably reduced, while inoculations with *Klebsiella* sp. strain IG3 improved their lengths (Sapre et al. 2018). The positive impact of the strain IG3 inoculation on the growth promotion and improved NaCl tolerance could be endorsed not only to its ACC deaminase activity but also to its IAA production in saline conditions. It is now recognized that IAA synthesizing PGPR increase the plant's access to nutrients and water (increased water use efficiency) and improve their absorption by altering root system (e.g., enhancing the number of root tips and the surface area of the root) that are anticipated to mitigate the stress generated by excess salt and drought in plants (Saravanakumar and Samiyappan 2007; Marulanda et al. 2009; Nabti et al. 2010; Sadeghi et al. 2012). In high-salinity environment (200–400 mM NaCl), *Pseudomonas* and *Bacillus* sp. produce IAA and improved the biomass in case of *Sulla carnosa* (Hidri et al., 2016). Similarly other strains of bacteria such as *Curtobacterium flaccumfaciens* E108 and *Ensifer garamanticus* E110 capable of producing IAA obtained from *Hordeum secalinum* encouraged plant biomass and resistance to salinity in barley (Cardinale et al. 2015). *B. licheniformis* HSW-16 and *Pseudomonas* both were able to diminish injury caused by salinity stress and encourage the growth of wheat (Singh and Jha 2016) and maize (Mishra et al., 2017) through the generation of IAA. Thus IAA that is exuded by bacteria is taken by plant cells; plus IAA that is endogenously produced by the plant can cause cell proliferation (Glick et al. 2007) which might be responsible for the well-developed root system.

Under salt stress IAA content decreases in plant cells which have several negative consequences such as the closure of stomata (Dunlap and Binzel 1996), disruption of cell wall plasticity, and expansion of cell wall (Ribaut and Pilet 1994). Salt-induced decline of IAA level in plants is compensated by IAA-synthesizing bacteria which amplifies their endogenous level in plants (Liu et al. 2013). Bacteria producing indole acetic acid and gibberellic acid also facilitates germination of seeds and plant growth in saline condition (Bal et al. 2013; Kang et al. 2014), by increasing alpha amylase activity in seeds, which leads to the breakdown of the starch into simple sugars. There is elevation in the content of phytohormones such as IAA and GA as well as development of salinity stress tolerance trait following treatment of radish seed with *B. subtilis* and *P. fluorescens* (Mohamed and Gomaa 2012). Increase in root-to-shoot by PGPR in salinity stress has been reported on wheat by *P. putida* (N21), *P. aeruginosa* (N39), and *Serratia proteamaculans* (M35) (Zahir et al. 2009); on red pepper seedlings by *B. licheniformis*, *B. iodinum*, and *Z. alba* (Siddikee et al. 2011); and on barley by *P. corrugate* CMH3 and *Acinetobacter* sp. CMH2 (Chang et al. 2014). Besides modulating the concentration of ethylene, auxin, and gibberellins, PGPR can also influence cytokinin ABA and salicylic acid level in plants under salinity stress. The root-associated bacteria belonging to genera such as *Arthrobacter*, *Bacillus*, *Azospirillum*, and *Pseudomonas* produces cytokinin and enhanced shoot and root biomass in soybean under salt stress (Naz et al. 2009). ABA synthesis is elevated during salt stress to close the stomata in order to minimize water loss through transpiration (Leung and Giraudat 1998). In saline soil shoot and leaf growth is inhibited by the higher concentration of ABA; however beneficial bacteria encourage plant growth in salt stress by suppressing the synthesis of ABA (Kang et al. 2014). During salinity stress plants usually respond by increasing endogenous ABA level (Albacete et al. 2008), but for rice plant inoculated with *B. amyloliquefaciens* RWL-1, the endogenous plant ABA content was appreciably reduced and SA content was enhanced. This elevated level of endogenous SA and reduced level of endogenous ABA may be linked with the resistance to salinity stress imparted to RWL-1-treated plants. Equivalent results were also shown by Khan et al. (2017) where the endophytic bacterial strain *Sphingomonas* sp. LK11 considerably mitigates salinity stress in tomato plants by regulating ABA and SA levels. In addition, *B. amyloliquefaciens* SQR9 inoculation in maize seedling also reduced ABA level which rises in salinity stress and maintained it at the normal level (Ilangumaran and Smith 2017). Cotton (*Gossypium hirsutum*) seed inoculation with *P. putida* Rs-198 increased plant biomass in salinized soil not only by the reduction in ABA accumulation and enhancement in endogenous IAA content. Both hormonal regulation induced the salinity tolerance (Yao et al. 2010). Thus it can be well understood that PGPR through modulation of the hormone-linked phenomenon in inoculated plants enhances the growth of various plants (Catroux et al. 2001; Saubidet et al. 2002).

2.4.4 PGPR Protect Photosynthetic Machinery from Salt Stress

High-salinity level has been demonstrated to cause a dip in osmotic potential in plants, which increases water efflux from cell leading to cell dehydration (Amjad et al. 2015). An extreme soil Na^+ level not only forces the water removal from the plant cell, causing a decline in cell turgidity, but also hampers the photosynthesis and carbon fixation (Yeo 1998). In order to maintain leaf water status during salinity, plants usually respond by closing their stomata to limit the water loss through transpiration (Munns and Tester 2008) which ultimately resulted in lower CO_2 level and its fixation during photosynthesis (Siddiqui et al. 2018). PGPR also regulate water potential and stomatal opening by affecting hydraulic conductivity and transpiration rate (Groppa et al. 2012). Maize plants supplemented with *B. megaterium* in salinity stress positively modulate root hydraulic conductivity compared to uninoculated plants, and this was linked with increased expression of two ZmPIP (plasma membrane aquaporin protein) isoforms (Marulanda et al. 2010). Furthermore, bacteria boost up the leaf water potential and leghemoglobin of nodule in alfalfa leading to salinity resistance in plants and improved nitrogen fixation (Martinez et al. 2015). The salinity disturbs the water availability and initiates physiological drought in plants. PGPR-inoculated plants, however, exhibit higher hydration or better water availability for various metabolic processes in contrast to control uninoculated plants as established by Shukla et al. (2012) leading to salinity tolerance in inoculated plants. The enhanced water content in PGPR-supplemented plants leads to improved water use efficiency and consequently amplifies CO_2 fixation and biomass (Mayak et al., 2004). Moreover, according to Nadeem et al. (2010) and Ahmad et al. (2013b), in saline environment due to bacterial supplementation, elevated relative water content (RWC) in wheat and mung bean was reported, respectively. Water use efficiency (WUE) refers to the ratio between the accumulated biomass and transpiration or water use. During salinity stress inoculation of tomato seedlings with *Achromobacter piechaudii ARV8* enhanced water use efficiency (Mayak et al. 2004). This may be due to enhanced photosynthesis during salinity stress which is justified by higher dry matter accumulation following bacterial inoculation. Higher plant dry matter accumulation in pepper (*Capsicum annuum*) plants supplemented with *Azospirillum brasilense* and *Pantoea dispersa* under salinity was related to enhanced stomatal conductance and photosynthesis (del Amor and Cuadra-Crespo 2012).

Chlorophyll content can be considered as a reliable index of resistance to salt-stressed tissue (Ali et al. 2014). Several crop plants exhibited a reduction in the contents of photosynthetic pigments (chlorophyll and carotenoids) during salinity and osmotic stress (Radhakrishnan and Lee 2013). Owing to the adverse effects of soil salinity, the chlorophyll content diminishes, which is due to activation of enzyme chlorophyllase (Reddy and Vora 1986), leading to breakdown of chlorophyll and photooxidation (Anjum et al. 2011). Besides this imbalanced Na^+/K^+ ratio also leads to reduced photosynthetic electron transport activity especially involving PSII (photosystem II) activity in chloroplasts (Sudhir and Murthy 2004; Chatterjee et al. 2018). The rate of carbon dioxide fixation decreases because salinity mediates stomatal closure leading to a decline in intracellular CO_2 concentration. The negative impact of salinity is not only confined to stomatal closure mediated reduction in photosynthates generation, but it also breaks down the photosynthetic pigments by decreasing the rate of biosynthesis or by enhancing the degradation of pigment (Sultana et al. 1999; Ashraf and Harris 2013). PGPR are also known to maintain CO_2 fixation rate by negating the effect of salinity on photosynthetic pigments. Oat seedling supplemented with PGPR demonstrated elevated chlorophyll content (Sapre et al. 2018). Equivalent reports of an amplification of chlorophyll content in PGPR supplied plant in NaCl stress were also observed by Shukla et al. (2012) and Bharti et al. (2014), respectively. Similarly, *Azotobacter* strain C5 and C9 inoculation improved the chlorophyll content highlighting a positive impact on growth and plant development (Rojas-Tapias et al. 2012). White clover plant inoculation with *A. brasilense* considerably improved the leaf chlorophyll content under both nonsaline and variable salt concentrations of 40, 80, and 120 mM NaCl (Khalid et al. 2017). Furthermore, Zhang et al. (2008) described that *B. subtilis* GB03 enhances photosynthetic capacity by increasing chlorophyll level in *Arabidopsis.* Higher chlorophyll content was also reported in ACC deaminase-containing PGPR-inoculated salt-stressed rice (Bal et al. 2013) and cucumber (Kang et al. 2014) compared to noninoculated plants. An elevated synthesis of chlorophyll in plants elevates the photosynthetic rate, and thereby starch generation, which might support plant growth improvement under stress conditions (Kang et al. 2014). Not only the chlorophyll contents but *F*v/*F*m values were also significantly enhanced in bacteria-inoculated sugar beet as compared with control plants, suggesting that chloroplast activity was promoted (Zhou et al. 2017) under salinity stress. The metabolite 5-aminolevulinic acid (ALA) synthesized by bacteria increases the rate of generation of ATP and NADPH by enhancing the chlorophyll fluorescence, maximum quantum yield (Fv/Fm), actual quantum yield (FPSII), photosynthetic electron transport rate (ETR), and nonphotochemical quenching (NPQ) value in rice seedlings in salinity stress (Nunkaew et al. 2014), and it also increases the efficiency of energy transfer in the light-harvesting antenna proteins to shield the photosynthetic apparatus (Sun et al. 2009). As a result of foliar application of ALA, various photosynthetic fluorescence indexes (e.g. YII, ql) (Wu et al. 2018) were recovered in cucumber seedling exposed to salinity stress which are associated with PSII efficiency, thereby highlighting the importance of PGPR supplied ALA to plant in saline environment. The rbcL gene codes for RUBISCO which has an imperative role in fixation of CO_2 by catalyzing the carboxylation of RuBP. Under salinity stress, gene rbcL was downregulated in oat seedlings in contrast to *Klebsiella* IG3 supplemented plants (Sapre et al. 2018). Carbohydrate metabolism and transport are also stimulated by beneficial microorganisms, which directly implicate source sink relations, photosynthesis, growth rate, and biomass reallocation. Seed-inoculated *B. aquimaris* strains under saline field conditions resulted in higher shoot biomass, NPK accumulation, and Na reduction in leaves due to enhanced total soluble sugars reducing sugars in wheat (Upadhyay and Singh 2015).

2.4.5 PGPR in Osmolyte Accumulation

Cell osmotic regulations also participate in bestowing stress tolerance. Compatible solutes such as proline and sugar maintain cell turgor and are well known as osmoprotectants (Weimberg et al. 1982; Mundree et al. 2002) which avert oxidative stress. To overcome initial osmotic shock after salinization, PGPR induce osmolyte accumulation which facilitates plant survival. Proline accretion is a frequent physiological response in higher plants exposed to drought and salinity (Delauney and Verma 1993) that help to sustain higher leaf water potential under stress and shield the plant against oxidative stress. Increased proline accumulation has been shown in soybean plants supplied with PGPR exposed to high-saline environment which mitigated salt-generated stress and induced growth (Han and Lee 2005). Zarea et al. (2012) also observed augmented proline accumulation in wheat after colonization of root with PGPR. Higher plants are shielded against salt and osmotic stresses due to elevated proline accumulation, not only by regulating osmotic pressure but also by stabilizing many functional units such as complex II electron transport and enzymes such as ribulose bisphosphate carboxylase/oxygenase (RUBISCO) (Mäkelä et al. 2000). In transgenic *Arabidopsis thaliana* with proBA genes derived from *B. subtilis*, enhanced proline synthesis conferred plants survival in saline conditions (Chen et al. 2007). Microbes accumulate large quantities of osmoprotectants in their cytosol exposed to osmolality fluctuations in their surrounding environment (Kempf and Bremer 1998). Under such circumstances, biosynthesis of osmolytes including proline, trehalose, and glycine betaines by PGPR is most likely to be quicker than their associated host plants. The compatible solutes synthesized by PGPR, absorbed through plant roots, help in maintaining osmotic balance and preventing cellular oxidative damage under saline conditions. Various PGPR (i.e., *Rhizobium*, *Azospirillum*, *Pseudomonas*, *Bacillus*, etc.), by donating osmolytes to plants, can enhance their tolerance to salinity (Casanovas et al. 2003; Zarea et al. 2012). In general, in response to drought and salt stress, osmolytes such as proline, glycine betaine, trehalose, glutamate, and soluble sugars are secreted by PGPR, which act in coordination with plant-produced osmolytes and encourage plant growth (Bashan and Holguin 1998; Rodríguez-Salazar et al. 2009; Sandhya et al. 2010; Vardharajula et al. 2011). Some contradictory results were also surfaced which demonstrated that proline accumulation diminished following PGPR inoculation in salt-stressed plants. Oat seedlings inoculated with PGPR under NaCl stress registered poorer proline accumulation in contrast to uninoculated seedlings (Sapre et al. 2018). Similarly, it was reported that the proline accumulation was suppressed after inoculation with *Streptomyces* sp. PGPA39 in salt damaged tomato plants (Palaniyandi et al. 2014). Alleviation of salinity stress occurred due to the reduction of proline content in *P. pseudoalcaligenes* and *B. pumilus* inoculated rice plant (Jha et al. 2011). It could be comprehended that PGPR supplied seedlings did not show the consequences of NaCl stress, as noted from the lesser proline buildup.

Co-supplementation of bean (*Phaseolus vulgaris*) with *Rhizobium tropici* and *Paenibacillus polymyxa* strain modified to overexpress trehalose 6-phosphate gene resulted in improved nodulation, nitrogen content, and plant growth. A microarray analysis of nodules revealed upregulation of stress tolerance genes suggesting that extracellular trehalose, which functions as an osmoprotectant, can induce salinity tolerance (Figueiredo et al. 2008). Salinity tolerance vital biochemical markers in plants are total soluble sugars (Ashraf and Harris 2004), which are osmolytes that aid in osmotic adjustment during various abiotic stresses (Sandhya et al. 2010). In NaCl stress, the amount of total soluble sugars (TSS) in oat seedlings supplied with PGPR inoculated was remarkably increased (Sapre et al. 2018). This verified the crucial role of soluble sugar in defending plants against the hazardous effect of salt.

2.4.6 PGPR Impact on Plant Nutrient Status

Nutritional imbalance hampers plant growth, development, and also the yield. Imbalances may result from the effect of salinity on the accessibility of nutrient, competitive uptake, and transport or distribution within the plant or may be caused by physiological inactivation of a given nutrient resulting in an increase in the plant's internal requirement for that essential element (Grattan and Grieve 1992). Salinity conditions drastically decreased the content of various plant nutrient elements with the exception of sodium and chlorine, which increased under salt stress (Karlidag et al. 2011). Research clearly indicates that salinity reduces N uptake (Feigin 1985). Phosphate accretion declines in plant facing salinity stress due to low phosphorous availability under such stressful condition (Sharpley et al. 1992); consequently plant develops P deficiency symptoms. Salinity can also modify Ca^{2+} uptake and transport leading to its deficiency in plants (Cramer et al. 1987). The most frequent mode of action executed by PGPR to raise the nutrient availability in the host plant is through the solubilization of phosphorus in the rhizosphere (Rashid et al. 2004). These rhizobacteria are vital for obtaining P from inadequately available forms and are significant for maintaining P in readily available pools. PGPR inoculations under salinity conditions also perked up the macro- and micromineral content in case of strawberry leaf and root in contrast to the unsupplemented plants. The highest N, K, P, Ca Mg, S, Mn, Cu, and Fe concentrations were registered from *Kocuria erythromyxa* EY43 followed by *B. atrophaeus* E6, *Staphylococcus kloosii* E37, and *B. sphaericus* E30 (Karlidag et al. 2013). In yet another study by Nadeem et al., 2009, it was established that ACC deaminase producing bacterium supplied maize plants absorbed higher quantities of N, P, and K as compared to noninoculated plants, which resulted in elevated K^+/Na^+ ratio in plants and thus proved beneficial for plant growth under salinity condition. N and K contents of *Bacillus* inoculated strawberry plants were found to be higher than uninoculated plants in presence of NaCl stress (Karlidag et al. 2011).

2.4.7 PGPR Increase the Availability of Volatile Organic Compounds for Plants

An important mechanism for the elicitation of plant growth is the production of volatile organic compounds (VOCs) by rhizobacteria. PGPR-derived VOCs are known to positively regulate plant growth, resulting in increased shoot biomass, and modulated stress responses. However, the perception of volatiles by plants and subsequently induced mechanisms require further research (Bailly and Weisskopf 2014). Exposure to VOCs reduced the total Na level by 18% and enhanced shoot and root growth of sos3 mutants in 30 mM NaCl (Zhang et al. 2008). The role of VOCs on *A. thaliana* growth stimulation was done by examining mRNA from *A. thaliana* seedlings, which were exposed to VOCs of *B. subtilis* GB03 through oligonucleotide microarray (Zhang et al. 2007). Almost 600 genes connected with metabolism, cell wall modification, auxin homeostasis, and stress response were identified. These studies clearly point out that VOCs play an essential role in processes related to growth and development of the plants. PGPR, *B. subtilis* GB03 inoculated with *A. thaliana* emits VOCs which can stimulate many different hormonal signals, which include auxin, brassinosteroids cytokinins, gibberellins, and salicylic acid (Ryu et al. 2003, 2005; Zhang et al. 2007, 2008). Apart from modulating hormonal homeostasis, VOCs also participate in the expression of ions transporters. It is now well known that during salt stress VOCs downregulate the expression of high-affinity K^+ transporter (HKT1) in the root and on the other hand upregulate it in the shoot which results in lower buildup of Na^+ ions inside the plant (Zhang et al. 2008). Another mechanism of PGPR-driven ionic homeostasis could be elucidated by exposure of volatile organic compounds (VOCs) derived from bacteria which are observed to regulate sodium ion concentration in plants. Furthermore, *Arabidopsis* plants supplied with *B. subtilis* GBO3 which produces VOCs were shown to exhibit salinity tolerance as compared to control plants. This elevated salinity tolerance is due to a decrease in root AtHKT1 expression in roots but upregulated it in the shoot which facilitates the root-to-root Na^+ recirculation (Shkolnik-Inbar et al. 2013).

2.5 Conclusions and Future Prospects

The most crucial limitations to world agriculture are the presence of abiotic stress conditions in the environment, the harmful impacts of soil salinity, and problems associated with tolerance mechanisms and ecological performance. Plant-associated microbes can confer resistance to such abiotic stresses. After acquiring the detailed knowledge of the mechanisms by which salinity stress adversely influence the physiology and metabolism of plants, one could able to improve the growth conditions for the cultivation and it would be a helpful tool for genetic engineering in future. For sustainable future, this is the need of hour to develop the salinity-tolerant varieties of economically important crops by exploiting genetic engineering and plant breeding, but it is a lengthy and expensive process. Contrastingly, the utilization of plant growth promoting rhizobacteria to alleviate salt stresses in plants could be a more cost-effective strategy, available in shorter time, and an environment-friendly option.

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Use of Plant Hormones for the Improvement of Plant Growth and Production Under Salt Stress

3

Rabia Amir, Faiza Munir, Maryam Khan, and Tooba Iqbal

Abstract

Phytohormones are specialized chemical messengers which play significant role in plant defense mechanisms against several abiotic stresses. Plants frequently face biotic or abiotic stresses which restrict their growth and productivity. Salinity, abiotic stress, acquires great significance, affecting plants in various ways, including oxidative burst, ions toxicity, altered metabolism and water stress. This ultimately obstructs the plant to reach its actual genetic potential. Recent investigations have unraveled the functional role of potential phytohormones as mediators between abiotic stress signaling and defense responses. These plant hormones have the capacity to induce numerous defense mechanisms by integrating the stress signals. Subsequently, the downstream responses are regulated in a coordinated manner to produce a robust defense response against salt stress. The present chapter highlights the role of hormones such as abscissic acid, gibberellic acid, cytokinins, brassinosteroids, jasmonates and salicylic acid for improving plant's tolerance and productivity under saline conditions.

Keywords

Phytohormones · Salinity · Stress signaling · Hormonal cross talk

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3.1 Introduction

Plant physiological and developmental responses are affected by various external and internal stimuli. Amongst external stimuli, environmental stresses either biotic or abiotic create disturbance in the intricate cellular network and initiate specific complex defense responses to maintain cellular homeostasis. Plant responses to stresses are highly specific and depend upon cellular, morphological, anatomical and physiological changes (Fahad et al. 2015). Pant adaptation to stresses involves regulation of metabolism including: protection of cellular components, regulation of cellular gene expression, accumulation of secondary metabolites (e.g. phenolics, sugars, proline, polyols etc.), antioxidants mechanisms and regulation of phytohormones (Parida and Das 2005; Munns and Tester 2008). Plants are the essential component of food chain and tackles different environmental constraints including flooding, heat, cold, salinity and drought stresses thus daunting food security of increasing population of human (Ashraf et al. 2018). Global agricultural land is threatened by high salt concentration of soil due to either natural or anthropogenic activities (Munns and Tester 2008). Salt stress adversely affects plant homeostasis and induces malfunctioning in seeds thus limiting its productivity e.g. rice is a salinity susceptible crop in which salt halts the growth of rice in its young stage limiting its productivity at mature stage (Lutts et al. 1995; Todaka et al. 2012).

Salinity disrupts the balance of phytohormones that mediate plant growth, development, acclimatization to variation, source/sink transition and nutrient allocation (Peleg and Blumwald 2011). Phytohormones act as signaling molecules that are considered as important endogenous molecules derived from plant biosynthetic pathway to control physiological responses and adaptation to stresses including salinity. There are several factors that control plant responses to salinity but phytohormones holds indispensable position as most of the adaptation related responses involve regulation of plant gene expression via fluctuation in phytohormones levels (Fahad et al. 2015). Phytohormones can work either locally and systemically to bring coordination in cellular activities (Wani et al. 2016). Group of phytohormones includes five classical hormones: cytokinins, auxin, ethylene, abscisic acid and gibberellins while methyl jasmonates, salicylic acid, brassinosteroids and strigolactones are the hormones with defined role in plant defense response to either biotic or abiotic stress (Peleg and Blumwald 2011; Kumar et al. 2015). The present chapter highlights the role of hormones such as abscissic acid, gibberellic acid, cytokinins, brassinosteroids, jasmonates and salicylic acid for improving plant's tolerance and productivity under saline conditions.

3.2 Salinity Affecting Plant Growth and Production

Salinity is an abiotic hazard for both glycophytic plants (plants that can grow healthily in soil with low salt concentration) and halophytic plants (plants that can grow in relatively higher salt). Salinity negatively affects plant's growth at various level of organization as a result of lower osmotic potential of soil, reduced photosynthetic and respiration activity, declined protein synthesis, sodium and chloride ion effects and alteration in nutrient uptake (Hussain et al. 2013; Mustafa et al. 2014). Salinity affects plant's growth by posing osmotic and ionic stress (Flowers and Colmer 2008). Influence of salinity on development and growth of various crops have been illustrated in Table 3.1.

Accumulation of salt in various part of plant inhibits plant growth in distinct manners. There are two well-documented phases of effects of salinity on shoot and leaves growth that includes osmotic phase and ionic phase. In osmotic phase (initial phase, also, referred as shoot salt accumulation independent effect), high salt concentration causes stomatal closure that leads to increased leaves temperature, decreased shoot elongation and overall reduction in leaves and shoot growth (Munns and Tester 2008). On the other side, ionic phase (toxic phase) of plant salinity responses include slower inception of plant growth, accumulation of salt in older leaves and early leave senescence. In long run, accumulation of toxic concentration of salt causes failure of shoot to tolerate salinity (Rajendran et al. 2009; Roy et al. 2014). The growth of plant roots is less susceptible to salinity than shoots, in spite of first organ of plant to encounter saline environment (Munns and Tester 2008). Furthermore, sodium ions (Na^+) accumulation in roots is one of the defense responses of woody plants to avoid salt toxicity in shoots under salinity (Rahneshan et al. 2018)

Salinity interacts with both micronutrients and macronutrients of plants thus interfering plant homeostasis (Iqbal et al. 2006). Salinity causes decrease in potassium (K^+) and calcium (Ca^{2+}) ions, amongst K^+ and Na^+ regulate plant growth and development by maintaining homeostasis (Parida and Das 2005). Potassium is macronutrient for plant and plays its role in marinating membrane potential, enzyme activation, controlling osmotic pressure, opening/closing of stomata, tropisms and maintenance of turgor pressure (Golldack et al. 2003). On other hand, Ca^{2+} act as secondary messenger thus control various plant cellular activities. In salinity, most of the K^+ ions interact with Na^+ ions to rectify stressful condition thus leading to K^+ deficiency while Ca^{2+} content depends upon plant physiology, plant's organs and the period of salinity stress (Melgar et al. 2006).

Salinity interferes with plant hormones and lead to delay or reduction in seed germination rate. Salt at higher concentration can inhibit germination while it can induce seed dormancy at lower concentration thus limiting the seed reserves (Iqbal et al. 2006). Many studies reported reduced seed germination leading to yield losses due to negative effects of salinity (Ahmadvand et al. 2012). For example, high salt concentration in wheat reduces germination rate, germination percentage, hypocotyl length, radicle length, fresh/dry weight of hypocotyl thus cause yield losses (Akbari et al. 2007). Perturbed osmotic potentials in salinity affect plants bringing alteration in metabolic activities of plant cell (Iqbal et al. 2006). Plant responses to salinity include leaf abscission, necrosis of shoot and roots, decrease in internode length, decrease in leaf area, thickness and succulence (Das et al. 2015). Physiological responses owing to reduced growth of plant under salinity are somehow related to decrease photosynthetic activity. Salt stress lead to stomatal closure that limit the activity of photosystem 2 (Kalaji et al. 2011). Uptake of salt causes increase in

Table 3.1 Effect of salinity on growth and development of various crop plants

Crops	Effect of salinity on growth and development	References
Oryza sativa	Reduced shoot dry weight, induced yield reduction, reduction in photosynthesis, stomatal closure, accumulation of dry matter in grains	Sultana et al. (1999); Wassmann et al. (2009)
Beta vulgaris	Glomerules germination, increased seed germination	Pinheiro et al. (2018)
Triticum aestivum	Shoot length, root length, shoot dry weight and root dry weight decreased with high salt	Naz et al. (2018)
Trigonella foenum-graecum	Wish yellow colouration of young leaves, shoots, biomass production decreased and diminution of the leaf number	Baatour et al. (2018)
Cucumis melo	Yield was substantially decreased, leaf pigments were affected	Akrami and Arzani (2018)
Mangifera indica	Toxicity and leaf abscission, reduced leaf fresh and decreased functional leaf number	Mahouachi (2018)
Brassica napus	High reduction in the fresh and dry masses of shoots and roots. Burning of leaves or other succulent parts and degradation of other pigments	Kholghi et al. (2018)
Rosa odorato	Effects on yield, stem length, stem thickness, and bud length except for bud diameter	Aydinsakir et al. (2018)
Helianthus annuus	More biomass to root and increased bud growth but halted the growth of plant.	Ma et al. (2017)
Glycine max	Delay in seed germination	Shu et al. (2017)
Cichorium spinosum	Leaf fresh biomass decreased and imparts changes on plant metabolism	Ntatsi et al. (2017)
Capsicum annuum	Reduced the appearance of the fruit by both decreasing the length and maximum width.	Qiu et al. (2017)
Cicer arietinum	Yield loss	Panta et al. (2018)
Hordeum vulgare	Burned leaf tips, yield loss, potentially inhibitory for translation of RNA	Panta et al. (2018)
Zea may	Burned leaf tips and growth reduction	Eaton (1942)
Gossypium hirsutum	Shoot growth depression	Eaton (1942)
Solanum tuberosum	Decreased tuber yield, retarded shoot growth and emergence, decline in photosynthesis, impaired nitrogen uptake	Geilfus (2018); Van Loon and Van den Berg (2003)
Nicotiana tabacum	Light green leaves and leaf margins curled upwards, lowering of burning quality, ash shows black colour, aroma and taste aggravate.	Geilfus (2018)
Lycopersicon esculentum	Restricted growth and impaired fruit setting, lack of shoot nitrogen, increased defoliation, blossom-end rot, reduced fruit water content, putative positive aspect on aromatic compounds in fruits.	Geilfus (2018); Papadopoulos and Rendig (1983)
Sorghum vulgare	Leaf burning and leaf-edge necrosis	Eaton (1942)
Fragaria ananassa	Increased total fruit yield and fruit firmness.	Esna-Ashari and Gholami (2010)
Phaseolus vulgaris	Leaf burning and abscission	Eaton (1942)

cytosolic osmotic pressure, accumulation of proline and soluble sugar (Flowers and Colmer 2008; Rahneshan et al. 2018). In short, high salt concentration has adverse effects on the productivity of plant and its growth due to ionic effects that limits water availability for plant and poor germination rate of seeds thus limiting production rate (Afzal et al. 2005).

Phytohormones are the important endogenous elements and the modulators of physiological responses that are vital for plants to combat salinity and lead to better adaptation (Skirycz and Inzé 2010; Khan and Khan 2013). Moreover, inadequate plant growth under salinity might be due to perturb hormonal balance and reduced endogenous production of plant hormones (Iqbal et al. 2012). Study of endogenous behavior and level of plant hormones that play significant roles to mediate plant responses to salinity could provide better understanding of tolerance mechanisms of plant under salt stress (Hamayun et al. 2010).

3.3 Plant Hormones and Salt Stress

Plants have developed several defense responses including stress related genes, reactive oxygen species (ROS) and hormones to cope up with severe environmental conditions. Plants have integration and coordination of complex signaling pathways which allow the generation of appropriate physiological responses for stress acclimation during salt stress. These signaling pathways include cascades calcium ions (Ca^{2+}), phytohomones and phospholipids which regulate plant development and growth during salinity. Plant hormones participating in various signaling networks during salt stress have been discussed in following subsections.

3.3.1 Abscisic Acid

Abscisic acid (ABA) was first discovered in 1960s and was considered to have role in promoting seed dormancy and leaf abscission. ABA plays numerous roles during normal growth and developmental stages of plants. It has role in the development of seed as well as seed dormancy and triggers the plant defense responses against environmental stresses leading to tolerance against them (Agati et al. 2011). ABA assists the survival plants under drought and salinity. This is due to the swift increase in the endogenous level of ABA under high salinity. Salt stress rapidly initiates the expression of ABA responsive genes including 9-cisepoxycarotenoid dioxygenase, Zeaxanthin oxidase, Molybdenum cofactor sulfurase and ABA-aldehyde oxidase. The increased levels of ABA support the plant to tolerate salinity and low water availability by stomatal closure and accumulation of osmoprotectants and proteins for osmotic adjustments (Xiong et al. 2002). Application of ABA can serve as important tool for improvement of crops nutritionally as well as economically as elevated level of endogenous ABA has led to enhanced tolerance against salt stress in *Phaseolus vulgaris*, *Brassica* sp. and *Zea mays* (He and Cramer 1996; Cramer and Quarrie 2002; Cabot et al. 2009).

For increasing the productivity of crops through application of ABA under salinity, it is critically important to investigate that how salt stress affects molecular and cellular processes leading to the generation of ABA signaling cascades. The expression of ABA responsive genes is controlled by Ca^{2+} dependent pathways. It has been observed that the expression pattern of *Oryza sativa* drought responsive genes such as OsCam1-1 and OsDSM2 resulted in an enhanced accumulation of ABA leading to tolerance against salinity in rice. The proteome study of these genes revealed their role in the synthesis of Ca^{2+} binding calmodulin and b-carotene hydrolase (Cabot et al. 2009; Saeng-ngam et al. 2012). Many studies indicated that salt stress triggers the Ca^{2+} dependent pathways and the related phosphorylation events which lead to the synthesis and accumulation of ABA. Subsequently in rice, salinity alleviates the production of MAPKs which have role in conferring tolerance against salt stress. MAPKs (Mitogen activated protein kinase) are the set of proteins: *MAPK,* MAPKK and MAPKKK which have critical role in stress responsive signaling pathways (Rao et al. 2010). Moreover, several *MAPKs* family genes including DSM1 and EDR (MKKKs) and MPKK1, 3, 4 and 6 were up-regulated in rice by ABA treatment and salt stress (Rao et al. 2010; Hadiarto and Tran 2011).

Tolerance to salinity can either be triggered by ABA independent or dependent pathways (Ryu and Cho 2015). ABA independent and dependent pathway genes are regulated by specific transcription factors (TFs). *ABFs, MYBs* and *MYCs* transcription factors directly bind to ABA dependent and salt stress responsive genes by binding to MYCRS (CAnnTG) and ABA responsive elements (ACGTGGC), respectively (Shinozaki and Yamaguchi-Shinozaki 2007). On other hand, *NAC* and *DREB2* (AP2/ERF) act through ABA independent pathways and regulate salt responsive genes (Shinozaki and Yamaguchi-Shinozaki 2007). TFs bind to the promoter region of ABA responsive genes and lead to the inactivation of type 2C protein phosphatases like *ABI2* and *ABI1*. Their inactivation triggers the action of *SNF1-type kinases* which target the ion channels and ABA dependent gene expression (Raghavendra et al. 2010). Therefore, ABA is crucial in the signal transduction and further downstream processing leading to salt stress tolerance in plants.

3.3.2 Brassinosteroids

Brassinosteroids (BRs) are important group of phytohormones which regulate many important processes of plant's growth and development. Structurally they are similar to animal steroid hormones which are involved in pollen tube formation, photosynthesis, leaf bending, protein and nucleic acid synthesis, vascular differentiation, stress response as well as other important processes during the plant growth phase. The protective roles of these compounds on the plants have been elucidated in numerous stresses including salinity, drought, pathogen infection and oxidative stress (Fariduddin et al. 2013).

BRs can serve as potent solution for improving crop productivity under the challenging stress of salinity. An exogenous treatment of brassinosteroids can modify the plant's anti-oxidative system and lessen the effects of several abiotic stresses, particularly salinity (Zhang et al. 2007; Shahbaz and Ashraf 2008). During salt stress, BRs act as a plentiful nitrite reservoir and increase the activity of pivotal enzymes such as Nitrate reductase which are involved in transport of nitrogen to the developing parts of plant. The activity of Nitrate reductase overcomes the harsh effects of salinity to a large extent by restoring the chlorophyll content and improving the development of growing plant shoots (Anuradha and Rao 2003). The exogenous application of 24-Epibrassinolide (24-EBR) has been shown to improve the plant's tendency to survive under stressful conditions due to increase in the activity of anti-oxidative enzymes such as Catalase in *Arachis hypogia*. Moreover, they enhance the photosynthesis and growth of plants under salinity in both susceptible and tolerant plant varieties. However, the effect of treatment of BRs in mitigation of salt stress is observed to be more on salt tolerant varieties than salt sensitive varieties (Shahbaz and Ashraf 2008). It is also notable that under normal physiological conditions, BRs have no significant effect on cellular structure but they substantially reduce the damage occurred to nuclei and chloroplast under saline conditions. This demonstrates that, the role of BRs is specifically increased under salt stress conditions and allows the plant to survive better under such conditions.

The protective role of BRs has been reported during photosynthesis and seed germination against salt stress (Fariduddin et al. 2013). Salt stress is renowned for its adverse effects on photosynthetic apparatus since it largely inactivates important photosynthetic enzymes such as PEP-carboxylase, Rubisco and Sedoheptulose-1,7-bisphosphatase (Sasse 1997; Nogués and Baker 2000; Lefebvre et al. 2005). It has been increasingly reported that BRs activate Rubisco (Ribulose-1,5-bisphosphate carboxylase oxygenase) and thereby increase its activity and carboxylation rate under salinity (Yu et al. 2004). Moreover, BR application enhance the activity of photosystem II in wheat and lessened the harsh effects of salinity on photosynthetic pigments (Anuradha and Rao 2003; Shahbaz and Ashraf 2008). Salinity is also known to cause a significant reduction of chlorophyll content due to enhanced accumulation of chlorophyll degrading enzymes (Reddy 1986). The application of 28-Homobrassinolide (28-HBL) significantly enhance the content of photosynthetic pigments such as chlorophyll and help the plant to regain its growth (Yu et al. 2004). This depicts the BRs role in possible mechanism involved in the synthesis of pigments by activating their transcription or translation (Bajguz 2000).

In many important crops, an enhanced growth and yield was observed upon application of BRs under saline conditions. The BRs application increases the yield and numbers of pod in leguminous crops (Rao et al. 2002). Similarly, treatment with BR has also increased the total yield and growth rate in rapseeds grown under salt stress (Hayat et al. 2000). 28-homoBL lowered the effects of salinity on *Vigna radiata* (Mung been) by up-regulating the activity of antioxidative enzymes, improving fluorescence and the photosynthetic rate (Hayat et al. 2010b). The enhanced tolerance due to BR application under salinity stress can be correlated with the cross-talk of BRs and other stress responsive phytohormones such as SA, auxin (Dhaubhadel et al. 1999). Numerous studies have reported that the stress responsiveness of BRs is due to its wide range of interactions with other plant hormones which gives rise to complex diverse signaling pathways leading to the stress tolerance (Divi and

Krishna 2009). The cross-talk between SA and BRs in conferring salt tolerance was confirmed when SA-insensitive npr1-1 (Non expressor of pathogenesis-related Genes1) mutants did not exhibit tolerance to salinity upon exogenous application of BRs (Divi et al. 2010).

BRs can also cross talk with ABA to regulate responses towards many abiotic stresses including salinity. During salinity, ABA induce growth arrest in seedlings due to activation of ABI5 (ABA INSENSITIVE 5) gene. The ABA mediated growth arrest of seedlings enables the plants to survive stress conditions (Lopez-Molina et al. 2002). Studies have shown that an exogenous application of BRs antagnonize the effects of ABA by attenuating the outputs of ABA signal during seedling development (Zhang et al. 2009). The underlying mechanisms behind the antagonistic action of BRs and ABA have been elucidated in studies where ABI2 (ABA INSENSITIVE 2) induced the ABA signaling pathway which ultimately increase the phosphorylation of BES1 (Protein brassinazole-resistant 2). This indicates the role of ABA in inhibiting the signal output of BR by triggering the expression of BIN2 kinase (Zhang et al. 2009). These studies indicate the role of BRs in alleviating the effects of salinity but the exact mechanisms through which they improve plant antioxidant capacity is still not clear.

3.3.3 Auxins

Auxins constitute a powerful group of plant hormones which are naturally synthesized by all plants. They help the plants to reach optimum growth and development by regulating the organogenesis, cell elongation, vascular differentiation and various other important growth events (Lau et al. 2008). Moreover, studies are revealing the roles of auxins in regulating various developmental programs under various abiotic stresses including salinity. However, the exact mechanism of auxin signaling which influences the plant developmental reprogramming under salinity stress is still not clear (Ryu and Cho 2015). Studies depicted that auxins suppresses seed germination under high salinity. The negative role of auxin under high salinity is due to incorporation of auxin signaling into the NTM-2 transcription factor (a NAC protein) mediated stress signaling which modulates seed germination under high salinity (Jung and Park 2011). However, this negative effect of auxin on seed germination might serve to provide protective role to combat the effects of salinity at early stages of plant development.

The levels of auxins have been cited to be reduced in several crops plants including rice and tomato under salinity (Kazan 2013). Around 75% reduction in auxin concentrations were seen in tomato when grown under salt stress. Another study conducted on root development in *A. thaliana* showed that under high salinity, the auxin accumulation and distribution patterns are altered in such a way that it remodels the root architecture (Liu et al. 2009; Petrussa et al. 2013). This suggests that auxin redistribution might have influenced reductionin plant growth under salinity stress. However, further research is required to be carried on to better illustrate the mechanism of auxin induced developmental responses during salinity stress.

3.3.4 Cytokinins

Cytokinins (CKs) were initially known to induce cell division of many plant tissues. However, presently they are considered to be important compounds involved in a widespread array of plant responses related to development such as anthocyanin production, shoot differentiation, leaf senescence, nutrient mobilization and chloroplast biogenesis (Hwang and Sheen 2001). CKs are reported to be synthesized in the developing seeds and root tips from where they are transclocated to the shoot to regulate various developmental processes (Zahir et al. 2001). Cytokinins regulate plant's growth and development under both biotic and abiotic stresses. An exogenous application of cytokinins on plant seeds can improve the plant growth during salt stress since it up-regulates the production of several antioxidative enzymes (Javid et al. 2011). An increased tolerance towards salinity was observed in egg plants via enhanced proline accumulation upon exogenous treatment with CKs (Wu et al. 2014).

CKs reduction in root and shoot region under salt stress have been reported in various studies. This reduction in CKs can affect the network of stress responsive genes by altering their expression patterns to better acclimate under salinity (Nishiyama et al. 2012). The decrease in CK levels under salinity can be reflected as a limiting factor for plant to combat salinity stress. Identical findings were attained, when Kinetin, a synthetic cytokinin, was found to induce seed dormancy in crops such as cotton, barley and tomato (Javid et al. 2011). Moreover, kinetin treatment improved the wheat seedlings growth under salinity. An exogenous application of Kinetin on wheat seedlings dramatically reduced the effects of salt (Naqvi et al. 1982). Moreover, application of kinetin on potato seeds prior to the induction of salt stress considerably inhibited plant's growth (Abdullah and Ahmad 1990). These positive findings suggested the possible role of kinetin in reducing the salt induced damage to plant by scavenging the free radicals and strengthening the plant's antioxidative defense system (Javid et al. 2011).

Although above finding suggest a potential role of CKs in alleviating the salt-induced damage to the plants, however some studies report contradictory results. An exogenous treatment of kinetin in bean plants lowered the plant growth and reduced the harsh effects of salinity (Kirkham et al. 1974). An exogenous treatment of another cytokinin benzyl adenine (BA), lowered the growth of salt sensitive Barley varieties under salt stress. However, antagonistic results were obtained in salt-tolerant barley varieties where BA treatment enhanced the shoot/root ratio, growth rate and total endogenous CK content under saline conditions (Kuiper et al. 1990). Some CK receptor mutants such as AHK3, AHK1 and AHK4/CRE1 play a negatively respond to osmotic stress during ABA signaling during stress (Tran et al. 2007). Since CK deficient *Arabidopsis* mutants exhibited greater tolerance to salinity with an ABA hypersensitivity and increased cell membrane integrity, as compared to CK-sufficient plants. Moreover, the transcript levels of CK-responsive receptor genes were differentially regulated during osmotic stress which suggested a functional role of CK receptors in modulation of stress responses (Nishiyama et al. 2011). While in many other plant species, CK receptors were modulated in such a way that depicted their negative involvement in response to osmotic stress.

It can be deduced that the antagnostic behavior of CKs might be due to crosstalk with phytohormones as ABA which eliminate tolerance in plant to salt stress (Javid et al. 2011). There are many studies supporting the crosstalk among cytokinins and stress responsive phytohormones and signaling pathways which modulate plant responses under salinity (Nishiyama et al. 2011, 2012). The antagnonistic activities of ABA and CKs have been demonstrated in several important growth and physiological activities such as plant acclimation in abiotic stress conditions (Zdunek and Lips 2001; Chang et al. 2003). For example, during most of the abiotic stresses, ABA helps the plants to acclimate better through stomatal closure, induction of leaf senescence and the enhanced biosynthesis of several osmoprotectants. However, CKs display an opposite behavior where they delay leaf senescence and stomatal closure during stress conditions (Chow and McCourt 2004; Finkelstein et al. 2002; Werner et al. 2006). These studies indicate that CKs behave in diverse manners during stress conditions depending on the kind of stress as well as involvement of other signaling and hormonal pathways. Considering these roles of CKs as key mediators of plant responses during salinity, CKs can also serve as excellent target of genetic manipulation to obtain salt stress tolerant plant varieties. However, maintenance of an optimum balance of CK concentration to minimize the possible adverse effects is critical to meet required goals.

3.3.5 Gibberellins

Gibberellins also called as Gibberellic acid (GA) are important plant hormones which play versatile roles in plants including pollen maturation, trichome development, leaf expansion, stem elongation, seed germination and flowering induction (Achard and Genschik 2009). Currently, around 126 different Gas have been reported in bacteria, fungi and higher plants and their number is increasing day by day. Some of the GAs play crucial roles in modulating the plant responses against abiotic stresses. Reduction in GA level has been reported to contribute in plant growth reduction upon exposure to abiotic stresses (Colebrook et al. 2014). GA biosynthesis is regulated by several environmental and developmental signals (Javid et al. 2011).

Amongst phytohormones, GA improves plant growth during saline conditions. The protective effects of GAs agsinst salinity have been discussed in this section. An exogenous GA treatment alleviated salinity stress by enhancing the seed germination rate in wheat, rice (Hasanuzzaman et al. 2013). Application of GA improved the length of roots by inducing the regulation of several salt-related proteins such as salt stress-induced protein (SALT protein), Glutamyl-tRNA reductase, Enolase, a hypothetical protein OsJ_025258, putative chaperonin 21 precursor, Phosphoglucomutase, Isoflavone reductase-like protein and Ribulose bisphosphate carboxylase (Wen et al. 2010). Moreover, GA treatment also enhanced the grain yield of two important wheat cultivars, named as MH-97 (salt sensitive) and Inqlab-91 (salt tolerant). The increase is yield is attributed to better modulation of ion uptake and hormonal homeostasis by GA3 under salinity (Iqbal and Ashraf 2013). In linseed (*Linum usitatissimum* L.) an exogenous application of GAs lowered the salinity induced damage to the plant (Achard et al. 2006). There was also an improvement in the content of osmoprotectants (glycine betaine) and antioxidative enzymes (catalase and superoxide dismutase) which shows the potential role of GA in improving plant's innate mechanism to combat salt stress (Khan et al. 2010).

GAs also serves as important hormones which cross-talk with other phytohormones to modulate plant's behavior in response to environmental stresses. However, the exact mechanism of GA cross talk with other hormones remained unclear for a long time. Recent studies report the involvement of some important proteins called DELLA family proteins in negative modulation of GA induced stress signaling (Achard et al. 2006). Though the exact mechanism of salt stress induced GA signaling is not clear, however the studies suggest that salt stress promotes a reduction in GA level and an increase in DELLA proteins (Achard et al. 2006; Achard et al. 2008b). Experimental results supporting these evidences were obtained where DELLA quadruple mutants (with loss-of-function) showed greater susceptibility to severe salinity whereas GA deficient mutants depicted a better survival under highly saline conditions (Achard et al. 2006). In addition, several DELLA mutants were analyzed for salt tolerance and growth parameters and results obtained were consistent with previous findings. The mutants exhibited robust association between flowering time transition, plant growth and salt stress susceptibility (Achard et al. 2008b). These studies show that DELLA accumulation negatively regulate GA signaling and enhance the plant tolerance to severe salinity.

3.3.6 Ethylene

Ethylene is a gaseous phytohormone that regulates plant's growth and developmental responses. It is a central regulator of plant responses towards a variety of environmental fluctuations (Abeles et al. 2012). The biosynthesis of ethylene can be modulated under several abiotic stresses including salinity. Ethylene biosynthesis can be influenced by salt and other abiotic stresses (Morgan and Drew 1997). The modulation of *ACS* gene (ACC synthase-a rate-limiting enzyme) has been seen at transcriptional as well as post transcriptional levels during salinity in several crops. For example the transcript levels of *ACS1* gene were enhanced in tobacco under salinity (Cao et al. 2006). Similarly, an upregulation in the expression patterns of *ACSs* were observed during both long and short term salinity in cotton (Peng et al. 2014). Consistent with these studies, the gain-of-function mutants etr1-1 (ethylene insensitive receptor) exhibited an enhanced sensitivity to salinity during plant development (Cao et al. 2007; Cao et al. 2008). On the other hand, mutants etr1-7 (with functional loss) showed an enhanced tolerance to salinity in *Arabidopsis* (Wang et al. 2008). Studies were, also, obtained in which ctr1-1 or EIN3 overexpressing (genes involved in ethylene signaling) mutants showed better seed germination rates and improved plant's growth and development against salinity and osmotic stress (Achard et al. 2006; Wang et al. 2007).

Treatment of plants with ethylene endowed them with an enhanced tolerance against salinity by exerting positive influence on several physiological processes such as a robust photosystem II function (Fv/Fm), improvement in chlorophyll a/b content and retention of K^+ in shoots and roots of *Arabidopsis* wild type (Col-0) (Yang et al. 2013). Similarly, ethylene also improved growth of tomato plants grown under salinity by exerting a positive regulation on developmental responses such as stomatal conductance, chlorophyll content index (CCI) and ion homeostasis (Amjad et al. 2014b). The ethylene-mediated tolerance to salt stress requires modulation of expression salt responsive genes. The overexpression of an important receptor involved in ethylene mediated stress signaling, *NTHK1* in *Arabidopsis thaliana* affect the expression of salt responsive genes such as *RD21A, rd17, VSP2* and *Cor6.6* (He et al. 2005; Cao et al. 2006). Moreover, the expression patterns of *NtERF1* and *NtERF4* (ethylene response factor in *Nicotiana tabacum*) were also higher upon overexpression of *NTHK1-1* in tobacco plants under high salinity (Zhou et al. 2006). These studies demonstrate the role of ethylene in mitigating the salt stress induced damage to the plant through ethylene mediated stress signaling leading to modulation of salt responsive genes.

3.3.7 Jasmonic Acid

Jasmonic acid (JAs) and methyl jasmonate (MeJA) are collectively known as jasmonates that are plant hormones derived from lipids and regulate plant responses from photosynthesis to defense (Farmer and Ryan 1990). These signaling molecules are considered to mediate extensive reprogramming of stress related genes and trigger defense responses against necrotrophic pathogens, insects, wounding and abiotic stresses (McConn et al. 1997; Thomma et al. 1999; Reymond et al. 2004). Recent molecular investigations have revealed the novel roles of jasmonates in salt stress tolerance. Several observations were made where salt tolerant varieties exhibited greater accumulations of JAs as compared to salt sensitive plant varieties (Kang et al. 2005). Moreover, salinity stress was also seen to enhance the accumulation and biological activity of JAs in several plants (Moons et al. 1997). Under high salinity, jasmonates recovered salt induced damage to rice seedlings by improving its total dry mass (Kang et al. 2005). JAs also mitigated the salt induced damage to by improving the protein content and rate of carbon fixation in *Pisum sativum* (Velitchkova and Fedina 1998). There is an increasing interest in jasmonate mediated salt stress signaling due to their observed role in conferring tolerance to plant against salinity.

Phopholipase D (PLD) is an enzyme involved in JA biosynthesis, since it release linolenic acid which further stimulates JA synthesis (McConn et al. 1997). PLD activity has been associated with the important plant stress related responses since there are several evidences of its role in mediating stress related signal transduction pathways (Wang 1999). JA levels were enhanced in tomato cultivars under salinity stress. It is noteworthy that salt tolerant tomato cultivar-Hellfrucht demonstrated more increase in JA levels gradually as salt levels increased. On the other hand, in salt sensitive tomato variety-Pera, the JA levels started to decrease after 24 hours of salt stress induction (Kramell et al. 2000). These findings suggest a positive role of JAs in mitigating the salinity induced damage to plants.

Although the exact mechanism of JA induced salt stress signaling remained unclear. However, recently some advances were made in exploring the JA mediated stress regulation in plants and crosstalk between JAs and ABA in defense signaling. There are specific receptors proteins called SCFCOI1 which perceive the jasmonate signals and modulate the plant defense and growth responses through JAZ TFs (Jasmonate ZIM-domain transcription factors) (Kazan and Manners 2012). The JA mediated defense pathway works in such a way that JA triggers the proteolysis of JAZ transcription factors via SCFCOI1 mediated 26 s proteasome pathway. This proteolysis leads to direct repression of another important class of transcription factors, MYC2 which activate the expression of stress related gens (Kazan and Manners 2012). Studies reported the role of *MYC2* in regulating the expression of salt responsive genes. Several results consistent with these findings are reported where JAZ proteins like *OsTIFY1, 10, 6* and *9* are identified as salt responsive genes in *Oryza sativa* (Ye et al. 2009).

Several studies have reported antagnositic effects of JAs and ABAs during salt stress. Application of JAs inhibited the expression of *OsLEAs* gene in the presence of ABA (Moons et al. 1997). Moreover, some salt stress responsive genes were expressed upon exogenous treatment of JAs but not expressed when JAs and ABAs were applied simultaneously. This shows some inhibitory effect posed by ABAs on JA mediated expression of stress related genes (Moons et al. 1997). These studies suggest that there exists a strong antagnositic relation between JA and ABA signaling during salinity stress therefore, plants behave and acclimatize themselves differently depending upon their genotype and regulatory controls.

3.3.8 Salicylic Acid

Salicylic acid (SA) is a plant hormone (of phenolic nature) which is involved in several important physiological and developmental processes such as flowering, photosynthesis, nitrate metabolism and ethylene metabolism (Hayat et al. 2010a). SA also has an significant role in modulating plant responses against various biotic and abiotic stresses including salinity (Kaya et al. 2002). Genetic studies of Arabidopsis mutants showed that SA serves imperative role in modulating trichome development (Traw and Bergelson 2003). However, the effects of Salicylic acid on these developmental and physiological processes are not very significant and might not only be due to SA signaling, since SA crosstalk with other major hormones to modulate all these processes (Pieterse et al. 2009).

SA responsive genes are related to stress signaling pathways that ultimately lead to cell death. These genes encode several potential defense related proteins, antioxidants, chaperone, heat shock proteins (HSPs) and genes involved in the biosynthesis of potential secondary metabolites such as cytochrome P450 (CYP 450), *Cinnamyl alcohol dehydrogenase* (CAD), and *Sinapyl alcohol dehydrogenase* (SAD) (Horváth et al. 2007). The positive role of SA against salt stress has been well documented for several important crop plants including mung bean, bean and mustard (Azooz 2009; Hamayun et al. 2010; Nazar et al. 2011). Application of SA improved the growth of barley and mung bean by ehancing overall photosynthetic rate and improving the stability of cell membranes under high salinity (El-Tayeb 2005; Nazar et al. 2011). Reports suggests that addition of SAs in soil ameliorated the subsequent salinity effects on maize and mustard plants by not only decreasing the accumulation of Na^+ and Cl^- but also improving the overall health (Gunes et al. 2007). Moreover, SA has also been seen to improve the activities of several antioxidative enzymes such as *Ascorbate peroxidase*, *Superoxide dismutase*, and *Glutathione reductase* when NaCl and SA are applied simultaneously. Enhanced activity of these enzymes can be attributed to induction of salt induced defense mechanism which reinforces the antioxidative system and increases the content of essential nutrients (Hamayun et al. 2010). Studies also suggested that the treatment of plants with SAs lowers the activity of *Catalase* due to which an enhanced accumulation of ROS occur in the cell (Horváth et al. 2007).

It can also be deduced that exogenous application of SAs is involved in the stimulation of important signaling mechanisms which enhance ROS accumulation. Interestingly, SA mediated defense signaling under salt stress was observed to be different across different plant species. For example, the CAT activity was substantially inhibited by the treatment of SA in tobacco, Arabidopsis and tomato; however it was not affected in rice and maize (Sanchez-Casas and Klessig 1994). It has been found in that Treatment with SA altered the levels of other phytohomones in wheat seedlings under salt stress. Since it enhanced the expression of IAA and ABA but did not influence the levels of cytokinins under salinity (Sakhabutdinova et al. 2003). This indicates that there can be a possible role of SAs in crosstalk with other plant hormones to develop effective anti-stress mechanisms and acceleration of plant growth under various stress conditions. These studies make SA a potential compound for reduction of not only salinity but also other abiotic stresses by getting a better understanding of SA mediated stress signaling and its crosstalk with phytohormones under various stresses.

3.4 Plant Stress Signaling and Phytohormones Under Salinity

Stress perception and signal transduction is essential for an effective coordination among multiple plant responses under stress situations. Under stress conditions various plant signaling pathways get triggered by specific signaling hormones which further activate the defense related pathways. Moreover, perception of stress leads to signal transduction via phytohormones as signal transducers (Harrison 2012). Furthermore, hormones interact (cross-talk) at various point of signal transduction by activating either phosphorylation cascade or common secondary messenger and form complex signaling network (Harrison 2012). Specific signaling pathways including ROS signaling, calcium signaling and hormonal signaling are regulated in plants under salt stress to produce downstream processes including tissue tolerance, ion exclusion and osmotic tolerance (Mittler et al. 2011; Suzuki et al. 2012).

Salinity leads to osmotic shock by triggering Ca^{2+} influx via calcium channels in cell membrane, calcium ions binding and phosphorylation of *calcineurin B-like protein-CBL interacting protein kinase* (CBL-CIPK) complexes and *calcium dependent protein kinases* (CDPKs) leads to activation of Ca^{2+} sensor proteins and ROS producing enzymes. ROS further activates Ca^{2+} influx that triggers activation of NHX1, Na^+/H^+ transporters and *salt overly sensitive kinase* (SOS1) that initiate Na^+ loading to xylem, transport of cytosolic Na^+, induction of osmoprotectants and osmolytes, retention of osmotic balance (Purty et al. 2008). Moreover, CDPKs mediated gene expression of antioxidant enzymes, osmolytes producing enzymes, SOS genes, and Cell adhesion molecules (CaMs) for signal amplification while calcium ions is pumped out of cell via Ca^{2+}-*ATPases* and calcium exchangers in tonoplast and cell membrane (Purty et al. 2008; Kudla et al. 2010; Batistič and Kudla 2012). Aquaporins transport hydrogen peroxide to cytoplasm thus promoting ROS signaling that control Na^+ accumulation (Mittler et al. 2011; Suzuki et al. 2012).

Phytohormones including SA, auxin, ABA, ethylene, GA and brassinosteroids interact with NO, Ca^{2+} and ROS to help the plant to acclimatize salt stress (Xia et al. 2015). For example, auxin triggers ROS and NO production to regulate hormonal signaling while ROS and NO accumulation in stressed condition causes degradation/inactivation of auxin and down regulation of transport related genes via MAPK cascades (Yadav et al. 2013; Xia et al. 2015). During salinity stress, decline in auxin signaling causes growth reduction but in cases ROS and NO cause up regulation of auxin (Shi et al. 2015). SA is another plant hormone that leads defense signaling involving transcriptional reprogramming during salt stress but the interplay between NO, ROS and SA is complex. NO and ROS induce SA production that regulate the accumulation of antioxidants and pro-oxidants (Mur et al. 2013). Moreover, ABA, among all pytohormones, performs a key role in primary metabolism and act as signal for various cellular receptors that activate ABA responses and interact with other hormones to mediate plant growth and metabolic signaling (Golldack et al. 2014). In the stress signaling, ABA interacts with GA to regulate plant stress response while GA mediates its signaling through binding of DELLA protein to GID1 (Golldack et al. 2013). Moreover, DELLAs acts as linking proteins in ABA, GA s and JA signaling that is important for developmental responses under stress conditions to regulate stress mediated responses (Achard et al. 2008a)

3.4.1 Cross Talk of Plant Hormones in Salt Stress

Several mechanisms through which plants combat the adverse effects of salinity, involve the physiological responses which exclude Na^+ ions from plant tissues and counteract osmotic stress. The ability of plants to deal with the salinity may differ from one species of plant to another. For example, halophytes are well adapted to salinity, these plants prefer salt environment by compartmentalizing excess salt in different tissues to minimize its harsh effects (Galvan-Ampudia and Testerink 2011). On the other hand glycophytes do not possess physiological features to withstand salinity. However, nature has bestowed the plants with some adaptive strategies to adjust their cellular and molecular mechanisms under salinity (Miyazawa et al. 2009).

Several studies have reported the role of phytoprotectants and complex signaling cascades in mitigating the effects of salinity. Now, it is clear that plant tolerance to salinity is a multifaceted phenomenon which involves action of multiple genes and several signaling cascades working in harmony to acclimatize the plants. Salt stress tolerance requires the action of various signaling elements and their pathways which include sensor molecules, signaling transducers, potential transcription factors, salt stress responsive genes and their respective metabolites (Zhu 2002). The complex network of signaling cascades are integrated in such ways that they trigger appropriate physiological and cellular responses which help the plants to better acclimatize under salinity. The accumulation of toxic Na^+ ions is restricted by maintaining ion homeostasis or osmotic adjustment through the action of several metabolites such as calcium ions (Ca^{2+}), phospholipids, or plant hormones. Plant salt stress signaling pathways mostly involve hormonal regulation or Ca^{2+} dependent modulation of enzymatic activities which independently or coordinately regulate plant growth and developmental responses.

Cross-talk of signaling pathways help the plants to control the expression of wide array of genes in spatio-temporal manner to trigger defense responses. Transcription factors (TFs) are converging points for almost all the signaling pathways and they can be synthesized or activated either directly through stress signals/signal transduction pathways or indirectly by the feedback mechanism regulated by other TFs (Liu et al. 1999; Fig. 3.1). Studies have reported the antagonistic or synergistic action of several phyto-hormones and their biosynthetic pathways for the modulation of plant physiological responses under salinity. Abiotic stresses trigger the accumulation of ABA which helps the plant to minimize the stress by promoting stomata closure, down regulating the genes that are involved in plant growth and triggering the biosynthesis of osmoprotectants. However, CK works antagonistic to ABA and trigger the responses which promote leaf senescence and stomata closure (Finkelstein et al. 2002; Chow and McCourt 2004; Werner et al. 2006). Moreover, CK deficient mutants exhibited hypersensitive response to ABA treatment during germination of seeds under salinity stress. Consistent with these observations, the mutants demonstrated better growth and salt stress tolerance (Nishiyama et al. 2011). These studies proposed that CKs interact with ABAs to eliminate salt stress tolerance which they alone can confer to plant. This is clear now that there is a regulatory loop involving both ABA and CK to modulate appropriate responses during salinity however more research is required to be conducted on signaling networks and transcriptional regulations involved during this crosstalk.

ABA has been also shown to crosstalk with JA during salinity induced stress signaling (Moons et al. 1997). Application of JAs inhibited *OsLEAs* gene expression in the presence of ABA (Moons et al. 1997). Moreover, some salt stress responsive genes were expressed upon exogenous treatment of JAs but not expressed when JAs and ABAs were applied simultaneously. This shows some inhibitory effect posed by ABAs on JA intermediated regulation of genes involved in stress tolerance

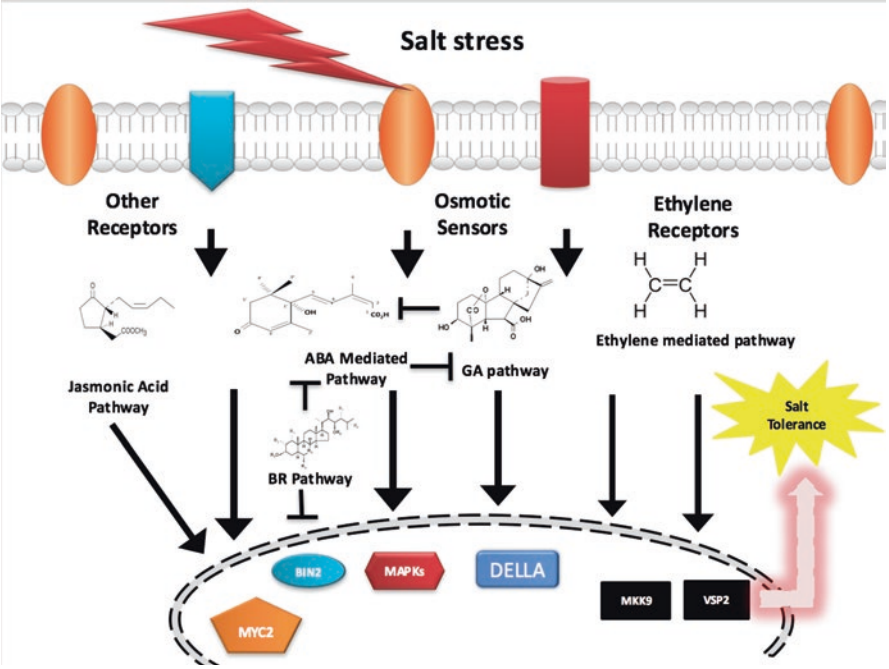

Fig. 3.1 A general mechanism of crosstalk between phytohormones and their transcriptional pathways during salt stress. (Adopted from Ryu and Cho 2015; Kaur and Pati 2017)

(Moons et al. 1997). Such studies proposed that there exists a strong antagnositic relation between JA and ABA signaling during salinity stress therefore, plants behave and acclimatize themselves differently depending upon their genotype and regulatory controls. Several studies postulate the cross-talk among BR and other phytohormones such as auxin, ABA and SA in modulating salt induced stress signaling (Dhaubhadel et al. 1999; Divi et al. 2010). Such regulation of hormones can either occur at hormonal biosynthesis level or the level of signal transduction that lead to stress tolerance (Nemhauser et al. 2006). The exogenous application of BRs has conferred salt tolerance in several crop plants. This can be correlated with the cross-talk of BRs with other stress related hormones such as SA, auxin and increase in expression of stress responsive genes (Dhaubhadel et al. 1999). The stress conferring ability of BRs are due to its wide range of interactions with other plant hormones which gives rise to complex diverse signaling pathways leading to the stress tolerance (Divi and Krishna 2009). These observations were strengthened by the studies made in which *SA-insensitive npr1-1* (Non-expressor of pathogenesis related genes1) did not exhibit tolerance to salt stress when upon exogenous treatment with BRs and vice versa (Divi et al. 2010). SA application either alone or with BRs, increases salt tolerance since SA has a role in salt tolerance (Fariduddin et al. 2013). Moreover, BRs cross-talk with ABA to regulate responses towards many abiotic stresses including salinity. During salinity, an enhanced level of ABA halts the growth of seedlings due to activation of *ABI5* (ABA INSENSITIVE5) gene. The ABA mediated growth arrest of seedlings and ensures the survival of plants under stress (Lopez-Molina et al. 2002). Literature has, also, shown that application of BRs antagnonize the effects of ABA by reducing the ABA signaling during seedling development (Zhang et al. 2009). The underlying mechanisms behind the antagonistic action of BRs and ABA have been elucidated in studies where *ABI2* induced the ABA signaling which ultimately increases the phosphorylation of *BES1* (protein brassinazole-resistant 2). This indicates the role of ABA in inhibiting the signal output of BR by triggering the expression of *BIN2 kinase* (Zhang et al. 2009). The role of BR in alleviating the effects of salinity has been reported in several studies but the exact mechanisms through which they improve plant antioxidant capacity and effect signaling pathways is still not clear.

3.4.2 Mechanism of Salinity Tolerance and Phytohormones

Plant stress response is largely relied on the underlying mechanisms of salt tolerance within individual crop species as is not a fixed feature (Almansouri et al. 2001). Salinity affects plant homeostasis in various ways thus there are various ways by which plants tolerate salt stress (Munns et al. 2012). Salinity responses in salt tolerant and sensitive plants have been explained in Fig. 3.2. Depending upon type of

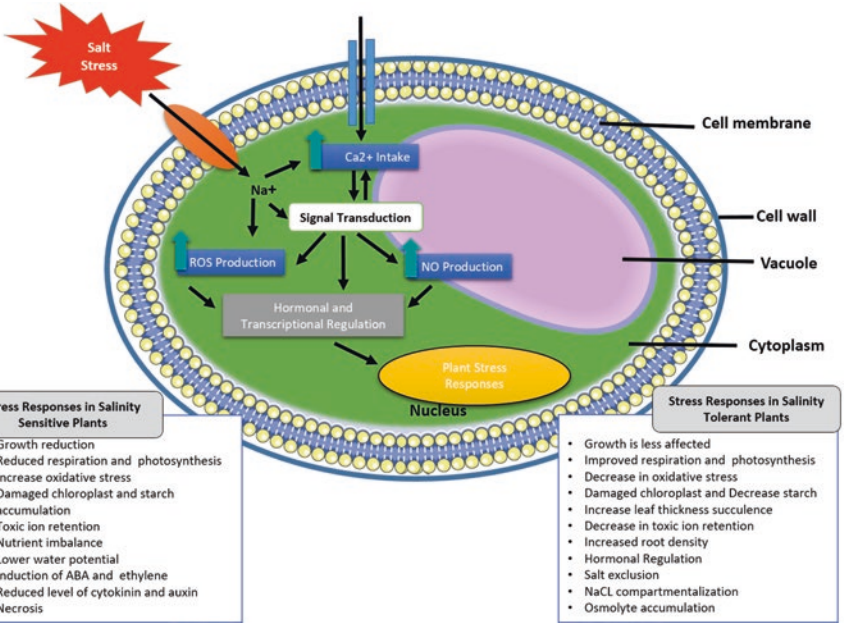

Fig. 3.2 Schematic presentation of steps involved in generating salt stress responses in salt sensitive and salt tolerant plants. (Adopted from Kosová et al. 2013; Muchate et al. 2016; Acosta-Motos et al. 2017)

response, plant responses to salinity has been categorized into three groups: (i) ion exclusion; (ii) osmotic tolerance, and; (iii) tissue tolerance (Roy et al. 2014). In osmotic tolerance, plant under salt stress regulates its systemic signaling to reduce shoot growth and initiate buildup of Na^+ ions. In ion exclusion, toxic concentration of Na^+ and Cl^- ions within leaves is reduced by transporting them to roots while in tissue tolerance, excessive salts are sequestered in vacuole to relief osmotic potential within cytosol (Mittler et al. 2011).

There are two well-documented phases of salinity effect that includes osmotic phase and ionic phase as explained earlier. In osmotic phase tolerance, distant signaling occurs through calcium signaling, Reactive oxygen species (ROS) signaling or electrical signaling (Maischak et al. 2010). Variation in osmotic tolerance may be attributed to distant signaling as they involve various initial stress perception and responses to stress (Plett and Møller 2010). In ionic phase that involves accumulation of salt in various tissues to reduce toxicity, various transporters and their regulator present in tonoplast and cell membrane get activated to avoid detrimental effects of high salt concentration and to regulate various biochemical process involve in osmotic adjustment and osmoprotection (Flowers and Colmer 2008; James et al. 2012).

Phytohormones, endogenous growth regulator, influence tolerance responses to salt by regulating seed germination, ion uptake, stomatal closure, membrane permeability, transport, growth and photosynthesis (Peleg and Blumwald 2011). Moreover, plant hormones regulate gene expression to encourage osmoprotection and compartmentalization of salt (Kalaji et al. 2011). Plant hormones have central roles to influence plant salt stress responses as they are involved in multiple processes taking place in a plant. Their crosstalk results into either antagonistic or synergetic interactions that also play critical roles to tolerate stress conditions (Peleg and Blumwald 2011). All the phytohormones play critical in regulating physiological responses that confer salt tolerance in salinity affected plants (Khan and Khan 2013). Amongst, ABA, SA, ethylene, nitric oxide (NO) and jasmonates are the stress specific hormones that mediate plant stress signaling. Auxin, gibberellin (GA), cytokinins and brassinosteroids have significant roles in salt tolerant plants by regulating physiological responses and gene expression (Iqbal et al. 2014). Auxin via auxin responsive genes alter its level and interact with responses related to salt stress while GA increase water level of seeding by marinating proteins level and interact with other hormones for effective salinity related responses through DELLA proteins (Bao and Li 2002; Iqbal et al. 2011). Ethylene and ABA as stress hormones accumulate under salinity and regulate salt responsive genes through ethylene mediated and ABA mediated signaling, respectively. Moreover, ABA causes increase in Ca^{2+} and K^+ ions, accumulation of soluble sugars, proline and decrease in Na^+/K^+ ratio and Na^+ and Cl^- ions while ethylene induces tolerance to salinity by regulating alternative respiratory pathway in plant and regulates signaling related to ROS (Wi et al. 2010; Gurmani et al. 2013). On contrary, Cytokinin works antagonistically to ABA and regulates various salt stress responses in plants (Iqbal et al. 2014). Jasmonates and brassinosteroids and NO confer salt tolerance in plants via mediating stress signaling and gene expression (Uchida et al. 2002; Khan and Khan 2013; Sharma et al. 2013).

SA and NO stimulate antioxidant defense system and regulate plant growth to maintain cellular homeostasis under salinity, furthermore, NO enhances the ratio of K^+/ Na^+ to lessen salt toxicity (Zhao and Schaller 2004; Nazar et al. 2011).

3.5 Application of Plant Hormones as Phytoprotectants

Salinity has posed need for effective stress management strategies due its adverse effects on the growth and productivity of plants. Several salt tolerance mechanisms are targeted by plant breeders to overcome hurdles in the plant productivity under salinity stress. Genetic resources of crop plants and their close relatives have been explored to get insight into salt stress tolerance, to enhance productivity with sustainable approach (Rahneshan et al. 2018). Various conventional breeding methods using molecular marker and 'omic' based tool, selection of salt tolerant varieties, insertional mutagenesis, mutation breeding and genetic engineering approaches have been exploited to develop salt tolerant crops but, now, usage of phytohormones have been evolving as a practical approach to deal salinity stress in agriculture (Khan et al. 2000; Amjad et al. 2014a; Roy et al. 2014; Sharma et al. 2013; Das et al. 2015). Phytohormones form a diverse group of plant endogenous regulators that held pivotal position in plant acclimatization to salinity. Plant hormones can act locally or systemically to maintain homeostasis for plant metabolism, so application of phytohormone to salt affected plants is an effective approach to maintain its productivity under stress (Wani et al. 2016). But the knowledge of individual hormone and its interaction with other phytohormones is crucial to confer adaptation to saline affected crop plants as their exogenous application have revealed prompt and momentarily variations at transcriptome level of genome (Chapman and Estelle 2009).

Salicylic acid is a phytohormone that regulates the production of phenolic compounds and participates in physiological responses of plant to stress. Its exogenous application to wheat plants has been found to increase cell division that lead to enhanced plant growth and wheat productivity. Moreover, SA treatment leads to increase ABA level in seedlings of wheat thus reduced the harmful effects of salinity on seedling growth by restoring normal level of plant hormones and help in the recovery after stress (Shakirova et al. 2003). On other side, ABA regulates stress responses and maintains proline accumulation in salt stressed plants (Shakirova et al. 2003). Exogenous application of auxin increases the germination rate and seed vigor of salt plant with exception. Moreover, auxin application enhanced hypocotyl length and fresh/dry weight of seedling (Akbari et al. 2007). Gibberellins (GAs) and ethylene have also been found to lessen the effects of salt stress in plant by inducing stress responses but their roles high influence by the actions of each other as GA increases ethylene synthesis while ethylene regulate GAs (Iqbal et al. 2012). Application of phytohormones and their effects on various salt affected plants have been listed in Table 3.2.

Priming of seeds with certain growth hormones, chemicals or reagents has been proved beneficial in germination under either stressed or non-stressed conditions. It has emerged as a sustainable strategy to confer tolerance plants under stress (Ashraf

Table 3.2 Application of phytohormones and their effects on various salt affected plants

Hormones	Plant	Responses of salinity affected plants to application of hormones	References
Auxin	*Arabidopsis thaliana*	Regulate the expression of salt responsive genes, enhance seedling fresh/dry weight and hypocotyl length	Bao and Li (2002); Akbari et al. (2007)
	Triticum aestivum		
Cytokinin	*Solanum melongena*	Increase in osmoprotectants e.g. proline content, decrease in ROS accumulation, enhanced the shoot/root ratio and growth rate	Wu et al. (2014); Javid et al. (2011); Kuiper et al. (1990)
	S. tuberosum		
	T. aestivum		
	Hordeum vulgare		
Gibberellins	*Brassica juncea*	Accumulation of osmoprotectants, enhance the seed germination rate, regulate the expression of salt responsive genes	Siddiqui et al. (2008); Hasanuzzaman et al. (2013); Wen et al. (2010); Achard et al. (2006)
	T. aestivum		
	Oryza sativa		
	Linum usitatissimum		
Abscisic acid	*O. sativa*	Reduce Na^+ and Cl^- content, increase the ratio of K^+ to Na^+, increase K^+ and Ca^{2+} content, accumulation of proline, soluble sugar content, improve tolerance to ionic stress	Gurmani et al. (2013); Amzallag et al. (1990); Yong-Ping et al. (2002); Srivastava et al. (2010)
	Sorghum bicolour		
	B. juncea		
	B. napus		
Ethylene	*Nicotiana tabaccum*	Decrease in ROS accumulation, enhance the content of photosynthetic pigments, enhance function of photosystem 2, retain of K^+ in shoots	Wu et al. (2008); Yang et al. (2013); Amjad et al. (2014a)
	A. thaliana		
	S. lycopersicum		
Nitric oxide	*O. sativa*	Induce *ATPase* expression, increase the ratio of K^+ to Na^+	Uchida et al. (2002); Zhang et al. (2004)
	Zea mays		
Jasmonates	*H. vulgare*	Induce gene expression, improve plant total dry mass, improve protein content and rate of carbon fixation	Kramell et al. (2000); Kang et al. (2005); Velitchkova and Fedina (1998)
	Pisum sativum		

(continued)

Table 3.2 (continued)

Hormones	Plant	Responses of salinity affected plants to application of hormones	References
Salicylic acid	*A. thaliana,*	Improve photosynthesis, inducing the activity of nitrate reductase and ATP sulfurylase, increase antioxidant metabolism, decrease in salt-induced K^+ loss, normalize salt induced membrane depolarization, decrease accumulation of Na^+ and cl^-	Jayakannan et al. (2013); Nazar et al. (2011); Azooz 2009; Gunes et al. (2007)
	B. juncea		
	H. vulgare		
	Vigna radiate		
	Z. mays		
Brassinosteroids	*O. sativa*	Increase in proline content, increase the activity of antioxidative enzymes, enhance the content of photosynthetic pigments	Divi et al. (2010); Kagale et al. (2007); Sharma et al. (2013); Yu et al. (2004); Hayat et al. (2010b)
	B. napus		
	A. Mutants		
	Arachis hypogaea		
	Cucumis sativus		
	Vigna radiata		

et al. 2018). Priming of seeds accelerates physiological activities to get prompt stress response. Priming of seeds especially with phytohormones regulates intricate plant signaling network that induce plant stress tolerance mechanism and enhanced plant growth, thus crop yield under stress e.g. priming enhances nutrient uptake through better root proliferation and physiological activities under salinity stress (Ashraf et al. 2018). Salinity causes decrease in seed germination but soaking of seeds, hormones have alleviated the adverse outcomes of salinity. For example, application of auxin to wheat seed has eased the salt stress during germination of seeds (Akbari et al. 2007). Moreover, priming of wheat with hormone SA has enhanced seedling growth and germination under saline environment while it was also observed that hormonal treatment decreased electrolyte leakage of water as compared to untreated seeds under salinity but ABA was not found to be very effective against salt tolerance (Afzal et al. 2005).

Other priming agents have been found to regulate endogenous hormonal level under both saline and non-saline conditions. In $CaCl_2$ treated wheat seed showed induction in leaf SA level while reduction in leaf ABA under salt stress while increased free auxin level was also observed in wheat. On other side, NaCl priming caused an induction in ABA while reduction in auxin and SA level in salt stressed wheat leaves (Iqbal et al. 2006). Hormonal priming is also effective to regulate oxidative stress during salinity, for example, ABA priming, not only, affects germination of seed but, also, reduce oxidative stress by inducing antioxidant enzyme e.g. peroxiredoxin, *Glutathione reductase* and *Superoxide dismutase* as reported in *Brassica napus* and *Brassica juncea* (Yong-Ping et al. 2002; Srivastava et al. 2010). Furthermore, hormonal priming caused the accumulation of phenolics and osmolytes as proline, betaine, soluble sugar and glycine (Srivastava et al. 2010).

3.6 Conclusions and Future Prospects

Salinity has becoming challenging issue of food security because of its greater magnitude and increasing population around the globe. Saline soil adversely affects the growth and development of plants by inducing osmotic and ionic damage. Plant respond to salinity by regulating its ions transport, production of osmolytes, compartmentalization of excess of salt to avoid toxicity and regulation of salt responsive gene and induction of antioxidant defense system. Moreover, plant regulates its ROS signaling, calcium mediated signaling and hormonal signaling to bring balance in plant homeostasis for optimum growth and production. Phytohormones that are endogenous regulators of growth, seed germination, metabolic and physiological activity play vital roles in plants against salinity stress. Plants have evolved several strategies to repressed hazardous outcomes of salinity stress. Many of these tolerance mechanisms against salinity have been exploited by plant breeders to enhance crop yield, grown in saline affected areas but usage of plant hormones as phytoprotectants is emerging as strategy to improve overall growth and production of agriculturally significant crops. Several phytohormomes are shown to be valuable for plant's growth and production after their exogenous application in various crop plants while hormonal priming of seeds has been found useful to enhance seed germination rate in salt affected areas. As exogenous and endogenous signals recognized by plants during stressed and non-stressed conditions are integrated, the plant response to stress is also linked by hormonal pathway. Thus, understanding of hormone and their interaction with other plant components is essential for devising effective management strategy and their use as phytoprotectants against salinity.

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4

Plant Growth Regulators and Salt Stress: Mechanism of Tolerance Trade-Off

Qazi Fariduddin, Abbu Zaid, and Firoz Mohammad

Abstract

With the advent of sophisticated technology and techniques in farming sectors, the problem of salt stress has increased manifold. Salt stress causes various alterations ranging from genetic to morphological level in crop plants. In order to improve salt stress tolerance, some sustainable strategies should be chalked out which on one hand engineer tolerance to salt stress and on the other side enhance photosynthesis, growth, and yield of crop plants. Plants have developed numerous strategies of tolerance to overcome the menace of salt stress. Among various practices adopted, the signalling crosstalk of plant growth regulators (PGRs) has received special attention recently among plant physiologists. In the present chapter, an appraisal has been prepared to explore the tolerance trade-off mediated by PGRs, viz. salicylic acid (SA), nitric oxide (NO), brassinosteroids (BRs), abscisic acid (ABA), methyl jasmonate (MeJ), and melatonin (Mel), in plants under salt-challenged environments. The present chapter highlights the role of PGRs for engineering tolerance against salt stress in various crop plants. Furthermore, the underlying mechanisms by which plants perceive signals of stress, which trigger signal transduction cascades, have also been elaborated. Moreover, the role of tolerance trade-off under salinity stress by PGRs, namely, SA, NO, BRs, ABA, MeJ, and Mel, has also been dissected in detail.

Keywords

Abscisic acid · Brassinosteroids · Nitric oxide · Salicylic acid · Stress tolerance

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4.1 Introduction

The population of the world is predicted to cross 9 billion marks in the first half of the twenty-first century, and if this scenario continues, the issue of obtaining food security for such a massive population would be difficult and likely to be compounded by dynamic climate as a greatest threat to our society (Thornton et al. 2014). Plants are exposed to various unfavourable environments because of their sessile nature; therefore, focus on elucidating the regulatory components and underlying mechanisms behind acclimation/adaptation to abiotic stress conditions would be of utmost importance and also to devise strategies in biotechnological and agricultural sectors for engineering-enhanced abiotic stress tolerance in plants. Out of the principal abiotic stresses, the problem of salt stress is posing a potential danger due to extensive farming and irrigation practices. Salt stress is characterized by the excess presence of soluble salt ions in soil environment and considered as one of the principal factors affecting growth and development of plants, thus causing great losses in terms of agricultural production (Chrysargyris et al. 2018; Jia et al. 2018). Soil salinity affects 20% of the land under cultivation and causes a significant reduction in yield of important plants (Qadir et al. 2014; Maswada et al. 2018). When electrical conductivity (ECe) of ions crosses 4 dS m^{-1}, the soil is then considered as saline (Munns and Tester 2008; Bertazzini et al. 2018; Table 4.1). Sodium chloride (NaCl), the main salt contributed through irrigation water or seawater, is responsible for soil salinity (Deinlein et al. 2014). Accumulation of ions in the vicinity of soil environment is due to improper practices adopted in farming and allied sectors (Rengasamy 2010). As a result of changing environmental conditions, the problem of salt stress is expected to aggravate further (Munns and Gilliham 2015). As a primary consequence, salt stress alters various metabolic activities in plants. Excess increase of sodium (Na^+) and chloride (Cl^-) ions in plant tissues poses several undesirable hyperionic and hyperosmotic effects (Fig. 4.1) which leads to disorganization of membranes and impairment of vital physiological and biochemical processes like photosynthesis, respiration, synthesis of proteins, uptake of essential nutrients, transpiration rate, sugar and lipid metabolism, and reduction in water potential which causes finally altered growth and development of crop plants (Khan et al. 2010a, b; Muchate et al. 2016; Ahanger and Agarwal 2017; Ahmad et al. 2018). Apart from this, salt stress induces oxidative stress in plants due to the excess production of a variety of reactive oxygen species (ROS) like hydrogen peroxide

Table 4.1 Categorization of salinity based on the range of electrical conductivity (ECe)

Category of salinity	Range of ECe (dS m^{-1})
Non-saline	0–2
Low salinity	2–4
Moderate salinity	4–8
High salinity	8–16
Severe salinity	16–32
Extreme salinity	More than 32

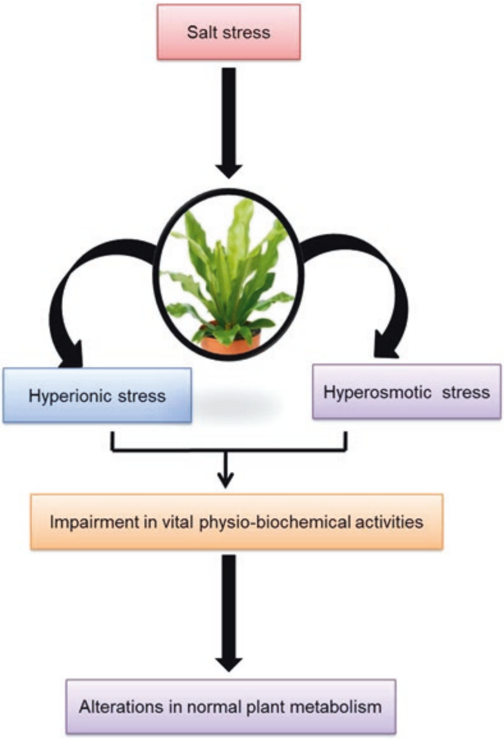

Fig. 4.1 Schematic representation depicting salt induced alteration in plant metabolism

(H_2O_2), singlet oxygen ($^1O_2$), hydroxyl radicals ($OH^{\cdot}$), and superoxide ions ($O_2^{\cdot-}$) particularly in the mitochondria and chloroplast which possess strong oxidizing potential causing deleterious effects to macromolecules like proteins, membranes, RNA, and DNA (Fariduddin et al. 2013a, b; Ahmad et al. 2018).

Plants stand healthy against oxidative stress induced by salts through activation of a battery of antioxidant agents such as α-tocopherol, ascorbate, and glutathione and enzymes like catalase (CAT), superoxide dismutase (SOD), glutathione peroxidase (GPX), glutathione *S*-transferases (GST), peroxidase (POX), dehydroascorbate reductase (DHAR), ascorbate peroxidase (APX), monodehydroascorbate reductase (MDHAR), and glutathione reductase (GR) (Ahmad et al. 2016; Hossain et al. 2017). SOD is a metalloenzyme which provides the first line of defence in response to overproduced ROS in plants. The SODs catalyse the dismutation of $O_2^{\cdot-}$ to H_2O_2 which is further acted upon by CAT and a variety of POX and convert it into water and molecular O_2 (Gill and Tuteja 2010; Das and Roychoudhury 2014; Hossain and Dietz 2016). Therefore, the two likely oxidizing agents, viz. $O_2^{\cdot-}$ and H_2O_2, are finally neutralized and converted to water. MDHAR and DHAR are key enzymes of the ascorbate-glutathione (AsA-GSH) pathway (Asada-Halliwell cycle) which represents an indispensable cellular component for maintaining ROS homoeostasis in different cellular organelles (Pandey et al. 2015) and control salt stress-generated manifestations in crop plants (Nazar et al. 2015). The first step of

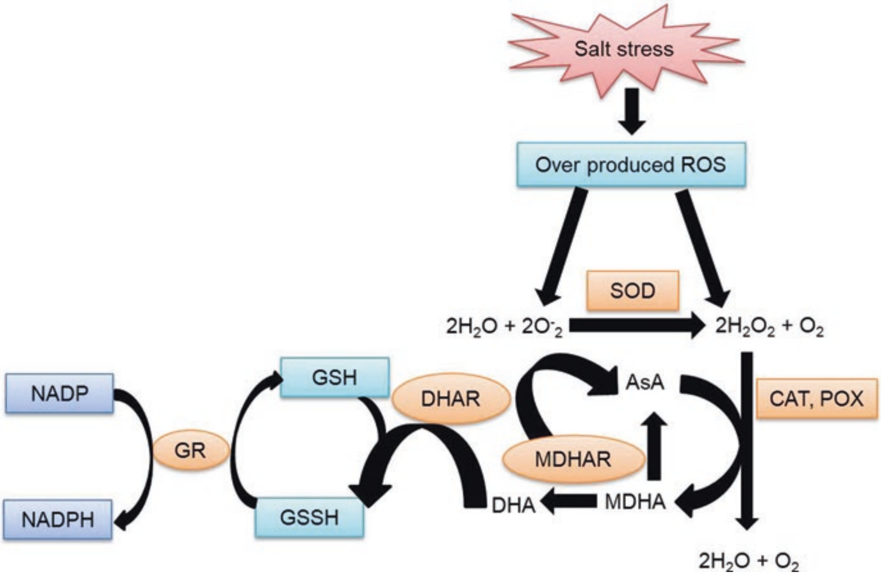

Fig. 4.2 A schematic representation of fate of salt stress generated reactive oxygen species (ROS) and their subsequent neutralization by antioxidants and enzymes of ascorbate-glutathione (AsA-GSH) pathway (Asada-Halliwell cycle)

the AsA-GSH cycle is the detoxification of H_2O_2 by APX, which is catalysed by the peroxidation of ascorbic acid (AsA) generating monodehydroascorbate (MDHA). MDHA undergoes two fates, either it is reduced back to AsA by the action of MDHAR, or it is converted non-enzymatically to form dehydroascorbate (DHA). The DHA are then converted to AsA by the catalytic activity of DHAR by using reduced glutathione (GSH) as the reductant which itself is regenerated from the oxidized glutathione dimmers (GSSG) by NADPH-dependent glutathione reductase (GR). The complete sequence of events in the formation of salt-induced ROS and their subsequent detoxification via the AsA-GSH pathway and other antioxidants are schematically represented in Fig. 4.2. Therefore, the present chapter highlights the role of PGRs for engineering tolerance against salt stress in various crop plants. Furthermore, the underlying mechanisms by which plants perceive signals of stress, which trigger signal transduction cascades, have also been elaborated. Moreover, the role of tolerance trade-off under salinity stress by PGRs, namely, SA, NO, BRs, ABA, MeJ, and Mel, has also been dissected in detail.

4.2 Causes and Origin of Salt Stress

The salt stress in rhizosphere could be induced naturally or by various anthropogenic activities such as irrigating crop plants with contaminated water or by the indiscriminate application of fertilizers and chemicals (Bartels and Nelson 1994).

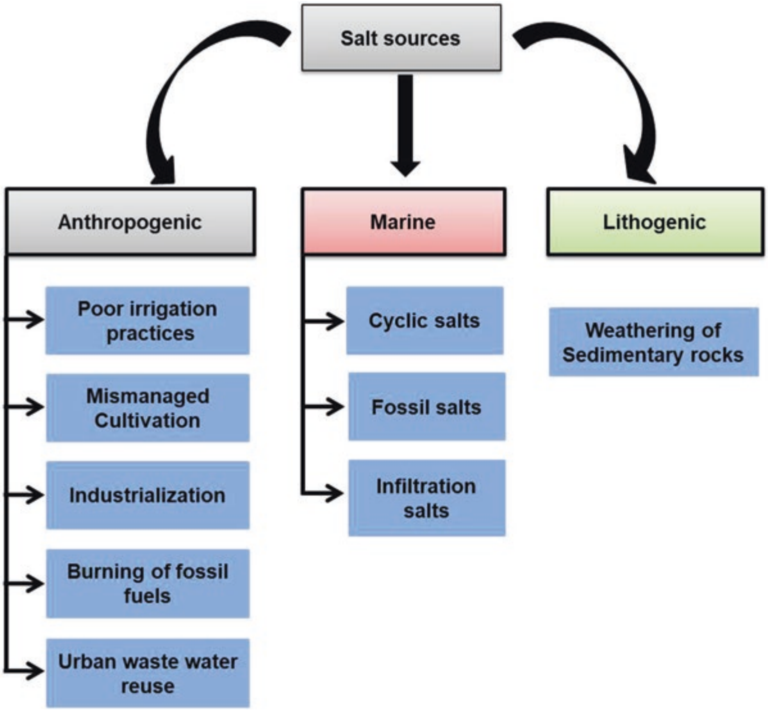

Fig. 4.3 Summary of various soluble salt ions are generated through major sources like anthropogenic, marine, and lithogenic activities

The soil salinity problem is aggravating further in the present times. As per the data given by FAO (2015), approximately 400 million hectares of land is contaminated by salt stress, in which natural origin constitutes 80% and rest 20% is from anthropogenic sources. Various kinds of salt ions are present around plant roots and some of them are essential nutrients required for normal growth and development of crop plants. However, when the rate of evaporation surpasses the precipitation process, salt ions get accumulated leading to high concentration in soil environments (Hachicha 2007; Taiz and Zeiger 2010). Moreover, soil salinity is further accelerating as a result of poor water drainage system in agricultural practices. Soluble salt ions are generated through major sources like anthropogenic, marine, and lithogenic activities. A brief schematic representation is illustrated in Fig. 4.3.

4.3 Role of Plant Growth Regulators: Salt Stress Signalling in Plants

Plant growth regulators (PGRs) are naturally derived signalling molecules, known to play significant and intricate roles to regulate growth, physiology, development, morphology, and responses to abiotic stresses (Wani et al. 2016). PGRs act as signalling agents in a very intricate manner allowing plants to maintain plasticity during growth and development and are hence considered as the principal factors in responses of plants to abiotic and biotic pressures (Bücker-Neto et al. 2017; Pal et al. 2018a, b). The role of PGRs is dependent on their bioavailability in plant tissues, which is further regulated by the rates of biosynthetic and metabolic pathways, furthering localization within the cellular and subcellular compartments, transport, and responses (Davies 2010). Regulation and modulations of PGRs levels could directly or indirectly impact an array of plants' physiological and molecular processes. Although certain PGRs have specific biological roles or responses, however, a number of studies have indicated that their signalling in plant tissues involves the complex crosstalk (Vanstraelen and Benková 2012). Nevertheless, plants have to face simultaneously different abiotic and biotic pressures, and hence, crop plants have to optimally perform to keep tune various physiological processes to the changing environment. The modulation of plants' physiological processes involves intricate coordination among biosynthesis, signal transduction, transport, and metabolism of PGRs and their interaction with transcription factors, responsive genes, and functional proteins.

PGRs are classified into several distinct classes such as cytokinins (CKs), auxins (AXs), ethylene, brassinosteroids (BRs), gibberellins (GAs), salicylic acid (SA), and abscisic acid (ABA), and they have been extensively searched in the past decades for their roles in plants in regulating growth and development under abiotic stresses (Fahad et al. 2015; Asgher et al. 2015; Wani et al. 2016). However, in addition to the existing class of PRGs, in recent times, new compounds like polyamines (PAs; a group of organic, aliphatic amines with aliphatic nitrogen structure) (Paul and Roychoudhury 2017; Pal et al. 2018a, b), nitric oxide (NO) (a gaseous signalling molecule) (Ahmad et al. 2016), jasmonates (Qiu et al. 2014), melatonin (Ke et al. 2018), and strigolactones (Ha et al. 2014) have also been implicated in the modulation of salt stress (Beligni and Lamattina 2001; Fariduddin et al. 2013a, b; Minoch et al. 2014; Zwanenburg et al. 2016). Nevertheless, perception of salt stress signal triggers the signal transduction pathways with PGRs which act as major players in regulating growth and development of crop plants (Harrison 2012). The impact of PGRs in modulating diverse physio-biochemical processes and physiological traits of various crop plants under salt stress have been unravelled extensively (Fatma et al. 2013). The concentration of these PGRs in the plants could be a deciding factor for enhanced tolerance/susceptibility because there is increased expression of stress-associated proteins under stress conditions in crop plants (Hamayun et al. 2010). Physiological and genetic studies have also shown the existence of crosstalk involving PGRs in modulating various developmental processes in plants (Li et al. 2018; Ahanger et al. 2018). Growth of plants under salt-persistent environments could be altered due to varying levels of PGRs (Iqbal et al. 2012). Jackson (1997) proposed that altered and diminished growth in plants under stressed environments is attributed to low endogenous levels of PGRs. Exogenous application of PGRs could be an efficient and practical strategy to impart salt stress tolerance in crop plants (Amjad et al. 2014). Supplementation of PGRs regulates many developmental aspects in the life cycle of plants via directly regulating gene

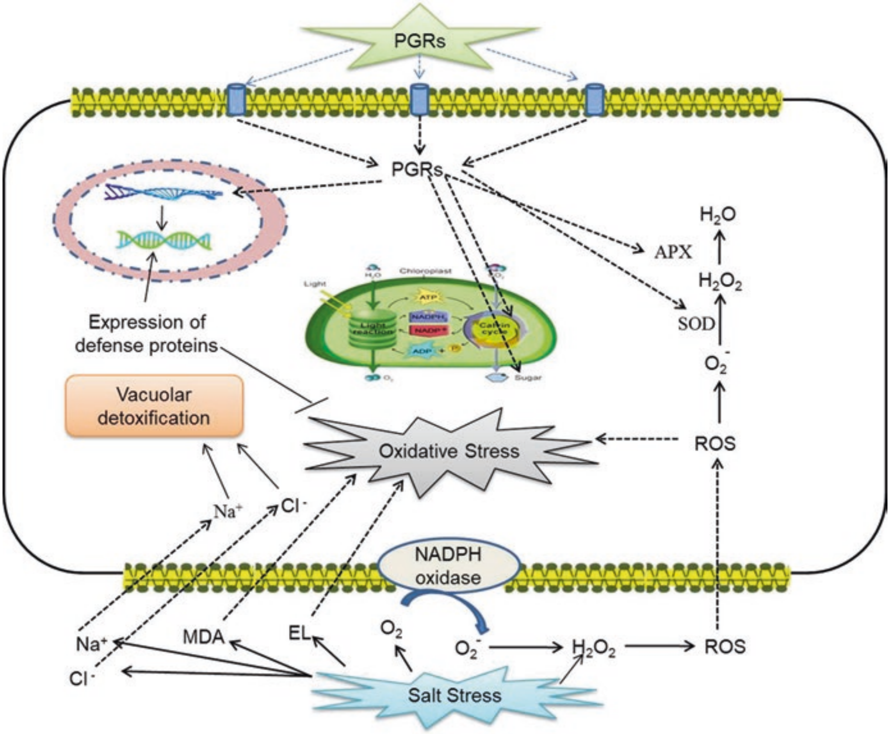

Fig. 4.4 Possible mechanistic functions of SA, NO, BRs, ABA, MeJ and, Mel in salt stress tolerance. Salt stress provokes oxidative stress as a result of elevated generation of reactive oxygen species (ROS), high electrolyte leakage and malondialdehyde content. PGRs provide salt stress tolerance by inducing the expression the defense proteins as well as by modulating major enzymatic and non-enzymatic components of plants' antioxidant defense system

expression or their interactions among specific DNA sequences, transcription factors, and other functional proteins (Chapman and Estelle 2009). Therefore, unravelling the beneficial role of PGRs individually or their trade-off during tolerance to salt stress could be very significant and deciphered mechanism could reveal the significant role of PGRs in conferring salt stress tolerance (Fig. 4.4). In the present chapter, the potential role of PGRs like SA, NO, BRs, ABA, MeJ, and Mel in alleviating adverse effect of salt stress have been summarized.

4.3.1 Salicylic Acid (SA)

It is a well-established phenolic PGR that has received a lot of attention among plant physiologists due to its diverse function in plants' responses to abiotic and biotic pressures (Hayat et al. 2007; Gururani et al. 2015). SA is known to act as an important regulatory signalling biomolecule in inducing plants' defence mechanisms against salt stress responses. The mitigative role of SA in imparting salt stress tolerance has been studied in diverse crop species, which includes *Vicia faba* (Azooz 2009), *Triticum aestivum* (Alavi et al. 2014), *Medicago sativa* (Palma et al. 2013), *Vigna radiata* (Khan et al. 2014), *Pisum sativum* (Singh and Dwivedi 2018), *Oryza sativa* (Kim et al. 2018), *Cucumis sativus* (Nie et al. 2018), and *Nitraria tangutorum* (Yan et al. 2018). SA imparts salinity tolerance in various crop species by employing different mechanisms. In *Torreya grandis*, SA conferred salt stress tolerance by activation of photosynthetic process and antioxidant defence system that eventually alleviated the inhibitory effect of oxidative stress (Li et al. 2014). Moreover, SA-mediated activation of photosynthesis, protection of morphological structure, and enhanced antioxidant system in *Dianthus superbus* were associated with the mitigation of the undesirable impacts of salt stress (Ma et al. 2017). In fact, the deficiency of SA in plants was regarded as the main reason of salt-induced alterations and reduction in the activities of antioxidant enzyme in SA-deficient *NahG* transgenic of *Arabidopsis* lines (Cao et al. 2009). In *Hordeum vulgare*, salt stress-accrued oxidative stress was diminished by the application of SA (50 μM) which resulted in lowering of malondialdehyde content (MDA, a marker of membrane-lipid peroxidation) and production of ROS (Fayez and Bazaid 2014). Priming of plants with SA could also be an important strategy for mitigating salt-induced injury which triggered a marked change in the expression pattern of members of GST gene family, viz. *SlGSTT2, SlGSTT3, and SlGSTF4* (Csiszár et al. 2014). External application of SA was found to improve tolerance to salt stress in wheat plants as a result of the upregulation of transcript levels of *GPX1*, *GPX2*, *DHAR*, *GR*, *GST1*, *GST2*, *MDHAR,* and *GS*, and further enhancement in the enzyme activities of AsA-GSH cycle (Li et al. 2013). In yet other recent study, SA-induced regulation of AsA-GSH pathway and ROS metabolism eventually led to enhanced salt stress tolerance in *Nitraria tangutorum* (Yan et al. 2018). In *Brassica napus* plants, exogenous SA (100 μM) minimized salt-triggered oxidative stress by boosting the antioxidant defence and glyoxalase systems (Hasanuzzaman et al. 2014). Khan et al. (2010) reported that exogenous SA application neutralized the negative impacts of salt-induced stress in mung bean plants by elevating the contents of mineral nutrients and antioxidative metabolism. Treatment of tomato plants with SA through roots has been found to mitigate the salinity-induced oxidative damage by interfering with stomatal response, rate of CO_2 fixation, and metabolism of carbohydrates (Poór et al. 2011). In *Arabidopsis*, SA induced salt stress acclimation by triggering marked changes in the levels of enzymes like GST and CAT (Horváth et al. 2015). Thus, it is apparent from the above discussion that SA imparts tolerance to salt stress in diverse crop plants by modulating vital processes in the life cycle of plants.

4.3.2 Nitric Oxide (NO)

NO is an endogenous and gaseous free radical signalling molecule which ubiquitously mediates complex alterations in plant growth and metabolism to impart abiotic stress resistance in plants by maintaining crosstalk with other PGRs at physiological, developmental, and biochemical levels (Asgher et al. 2017; Sami et al. 2018). There are various evidences which indicate that NO is involved in the alleviation of harmful effects of salt-induced changes in plants. Perhaps, the ameliorative character of NO in plant salt tolerance has been studied in diverse plant species, viz. cucumber (Shi et al. 2007), tomato (Hayat et al. 2013; Da-Silva et al. 2017), *Jatropha* species (Gadelha et al. 2017), strawberry (Christou et al. 2014), Indian mustard (Fatma et al. 2016), cotton (Kong et al. 2016), wheat (Kausar et al. 2013; Khan et al. 2017), Bermuda grass (Liu et al. 2016), and pea (Yadu et al. 2017), in which NO promotes growth, development, and photosynthesis and protects plants from salt-induced oxidative damage. NO control vital processes like photosynthesis under salt-induced stress in *Brassica juncea* plants (Fatma and Khan 2014). In addition, Fatma et al. (2016) reported that NO maintained morphology of thylakoids and increased size of chloroplast which improved photosynthesis and growth under the salt-challenged environment in *B. juncea* plants.

Under stress conditions, NO has been shown to facilitate the uptake and translocation of mineral nutrients, viz. K, Mg, Zn, and Fe (Dong et al. 2015). In two ecotypes of *Phragmites communis*, results of Zhao et al. (2004) indicated that NO function as an important signalling agent in inducing tolerance to salt stress by influencing the ratio of K^+ and Na^+ ions, which were dependent on the enhanced activity of the pump- H^+-ATPase located in the plasma membrane. Zheng et al. (2009) found that the NO pretreatment to *Triticum aestivum* cv. *Huaimai 17* maintained homoeostasis of K^+ ions under salt stress. They also found that exogenous NO supplementation improved amylase, SOD, and CAT but simultaneously decreased the MDA contents, H_2O_2, and ROS release in the mitochondria under salt stress. In chickpea plans, NO donor, S-nitroso-N-acetylpenicillamine (SNAP), has been evidenced to ameliorate the negative impacts of excess salt stress via improving leaf relative water content, photosynthetic pigment biosynthesis, osmolyte accumulation, and expression of genes associated with antioxidant defence system (Ahmad et al. 2016). In *Lycopersicon esculentum* seedlings, Wu et al. (2010) reported that NO alleviated salt-mediated inhibition of photosynthesis. NO (1 mM) treatment with *T. aestivum* upregulated the activities of enzymes, viz. GST, MDHAR, DHAR, GPX, CAT, and GR, and increased the content of GSH, AsA, under 300 mM salt stress (Hasanuzzaman et al. 2011). This NO-mediated boost in antioxidant enzyme activities and AsA-GSH contents caused a significant decrease of MDA and H_2O_2 generated due to salt stress. Similar NO-mediated salinity tolerance as a result of activation of the antioxidant defence system and ROS metabolism was reported in mustard (Gupta et al. 2017), pea (Yadu et al. 2017), and tomato plants (Wu et al. 2011). NO (300 μM) has been shown to delay salt stress-triggered leaf senescence which was reflected in terms of high chlorophyll values, net photosynthetic rate, and increased expression of *LHCB, SOS1*, *NHX1,* and genes associated with cytokinin biosynthesis, viz. *IPT1* and *ZR* and *iPA* genes, but decreased endogenous content of ABA and expression of its biosynthesis genes, *NCED2* and *NCED9,* in cotton under salt-challenged environments (Kong, et al. 2016). Hence, it is clear that NO plays a very fundamental role in conferring tolerance to salt stress in plants by regulating vital activities in plants.

4.3.3 Brassinosteroids

BRs are polyhydroxylated sterol-derived PGRs which are ubiquitously found in all plant species and are implicated in a monitoring broad spectrum of growth and developmental processes in diverse crop plants (Sirhindi 2013; Fariduddin et al. 2014; Ahanger et al. 2018). BRs are involved in the regulation of multiple plants' physiological, biochemical, and developmental functions which include elongation and division of cells, seed germination, differentiation of vascular tissues, senescence, reproduction, development of root and shoots, photomorphogenesis, and responses of plants to various biotic and abiotic pressures (Ahamed et al. 2014; Wei and Li 2016; Ahanger et al. 2018). 24-Epibrassinolide (24-EBL) and 28-homobrassinolide (28-HBL) are two main active forms of BRs which have been extensively studied due to their stability under field conditions and regulating the growth and metabolism of plants (Vardhini and Anjum 2015; Siddiqui et al. 2018). BRs have also been implicated to show the ameliorative role against salt stress in various species of plants, viz. *Oryza sativa* (Sharma et al. 2013), *Mentha piperita* (Çoban and Baydar 2016), *Cicer arietinum* (Ali et al. 2007), *Zea mays* (Rattan et al. 2014), *Vigna radiata* (Mir et al. 2015), *Cucumis sativus* (Fariduddin et al. 2013a, b), *Triticum aestivum* (Qayyum et al. 2007), *Gossypium hirsutum* (Surgun et al. 2015), and *Eriobotrya japonica* (Sadeghi and Shekafandeh 2014). BRs modify the plants' antioxidant defence system to counter salt stress effects in diverse plants species. In a study involving *Vigna radiata* plants, Hayat et al. (2010) reported that HBL alleviated the salt-induced stress by modulation of antioxidant defence system and proline content. Their study concluded with the observation that high salt stress caused a reduction in carboxylation efficiency, but increased electrolyte leakage and lipid peroxidation, which led to downregulation of the pigment system (PSII) activity. BRs' application to the salt-stressed seedling alleviated the damage via increasing the carboxylation efficiency and the activity of enzymes associated with the ROS detoxification system. In *Cicer arietinum*, Ali et al. (2007) reported the effect of HBL in amelioration of saline stress. Plants receiving HBL under salt stress exhibit high leaf nitrate reductase and carbonic anhydrase activities. The seedlings developed from seeds kept in an aqueous solution of HBR for 8 h had improved growth, photosynthetic pigments, and yield at 90-day stage. HBR also recovered the salt-induced decrease in nitrogenase activity and leghaemoglobin content. In groundnut cultivars, Trivedi and Illa (2016) studied the effect of BRs on protein profiling under salt stress. They observed that leaf protein content was reduced under salt stress, but when BR was applied, the protein content increased. They also found that the application of BRs under salt condition induced the synthesis of new resistant protein, which increased the intensity of the original protein bands and caused the appearance of an additional new band of proteins in PAGE. They concluded their study by observing that BRs are an ideal candidate for alleviating salinity-induced changes in groundnut plants. A study involving crosstalk of BRs and polyamines under salt stress in wheat plants showed that salt stress affected plant productivity by decreasing stability index of membranes, photosynthesis, leaf-relative water content, nitrate and chlorophyll contents, nitrate reductase and carbonic anhydrase activities, and carbohydrate and protein content (Talaat and Shawky 2012). However, the follow-up supply with 0.1 mg L^{-1}EBL circumvents the salt-induced changes and enhanced the productivity of wheat plants by significantly improving the above-mentioned parameters. In such plants, EBL affected the endogenous polyamines pools by influencing the activities of polyamine oxidase and diamine oxidase, which indicates a positive trade-off between polyamines accumulation and salt tolerance. In *Brassica juncea* plants, Hayat et al. (2012) reported the comparative effect of HBR and SA in enhancing salt (4.2 dsm^{-1}) stress tolerance. It was found that salt stress induced a significant reduction in gas exchange traits and plant growth parameters but elevated the proline concentration and leakage of ions. However, salt-induced negative effects were completely nullified by the combined application of HBL and SA. In yet another study, the effect of EBL in salt-stressed *Medicago truncatula* was studied in which it was found that the exogenous supply of EBL showed mitigative impacts in response to salt stress by improved level of polyamine (López-Gómez et al. 2016).Their results suggest the tolerance trade-off between salt stress and EBL and polyamine. Agami (2013) studied the interactive effect of SA and EBL on physiological and anatomical parameters in maize seedlings, in countering the deleterious effects of salt stress. Their results indicated that the stress imposed by salt resulted in a significant reduction in plant growth traits, water contents, photosynthetic pigment, soluble sugars, and activities of CAT, POX as well as on leaf anatomy. But, the combined application of SA or EBL mitigated the phytotoxicity of NaCl stress by improving physiological and anatomical parameters. In lettuce plants, Serna et al. (2015) worked out the role of BR analogue in preventing the adverse impacts of salt-induced stress through crosstalk of ethylene and polyamines. These results suggest an intimate tolerance trade-off between BRs and polyamines in imparting tolerance to salt stress in crop plants. Thus, it is imperative from these studies that BRs act as strong signalling agents which regulate tolerance to salt stress in diverse crop plants.

4.3.4 Abscisic Acid

ABA is a small sesquiterpenoid signalling molecule (Pilet 1998) and is classified as a PGR. ABA is commonly called as "stress hormone" which modulates plants' response to an array of stresses including both biotic and abiotic origin (Zhang 2014; Wani and Kumar 2015; Zhu et al. 2017). The ABA biosynthesis occurs de novo in plant tissues (Roychoudhury et al. 2013). ABA is a vital PGR that mediates the expression of stress responsive genes under salt stress conditions. There is rapid accumulation of ABA in roots than leaves under salt stress conditions in plants (Jia et al. 2002; Zörb et al. 2013). However, there is established role of ABA during salt stress, but the underlying mechanism of salt-induced accumulation of ABA is yet to be dissected in detail. In *Arabidopsis* and other crop plants, ABA biosynthetic mutants undergo wilting and later on die under prolonged salt stress, which concludes the modulatory role played by ABA under salt stress tolerance (Koornneef et al. 1998; Liotenberg et al. 1999). Salt stress triggered the gene expression, transcription factors, secondary messengers, and protein kinase/phosphatase which are induced by ABA. *AREB1/ABF2, AREB2/ABF4, ABF3,* and *MYB41* comprising key TFs are modulated under salt stress in vegetative organs of plants (Fujita et al. 2011). In addition, during salt stress, ABA regulates stress-inducible expression of genes at the epigenetic level by acetylation and methylation of histone proteins. There is a tolerance trade-off between salt stress and ABA signalling in plants. Chen et al. (2010) found that in *Arabidopsis*, ABA and salt stress conditions trigger activation of the gene markers and histone trimethylation and acetylation. ABA regulates the plant morphology under salt stress. Duan et al. (2013) showed that ABA induced the formation of lateral root growth under salt stress which was inhibited by salt stress. Yoshida et al. (2003) found that exogenously applied ABA improved the growth of *Chlamydomonas reinhardtii*. 50 μM (ABA) induced osmotic stress tolerance in *Atriplex halimus* seedlings through improved efficiency of stomatal conductance (Hassine et al. 2009). In *Salicornia bigelovii*, salt stress (0.005 to 500 mM NaCl) was negatively related to the ABA content in shoot tissues, with respect to water content and growth of plant suggesting that ABA-induced water stress conditions could retard growth at both the supraoptimal and suboptimal salinity levels (Ohori and Fujiyama 2011). In spring wheat, Afzal et al. (2006) studied the effects of ABA (10, 30, and 50 ppm), SA (50, 100, and 200 ppm), and ascorbic acid (50, 100, and 200 ppm), in alleviation of salt stress. Salt stress caused a significant reduction in fresh and dry mass of shoots and roots in plants. Priming of wheat plants with ascorbic acid and SA (50 ppm) improved salt tolerance, whereas the ABA was not efficient in recovering salt-induced damages in wheat plants. Similar results involving ABA (10^{-5}M) in two cultivars of wheat plants during salinity stress conditions were reported by Gurmani et al. (2007). It could be concluded that ABA is a vital signalling PGR that regulate the tolerance of plants under salt stress conditions.

4.3.5 Methyl Jasmonate

MeJ is a naturally occurring PGR and ubiquitously distributed in the plant kingdom. MeJ controls a wide range of plant growth and developmental activities in plants (Engelberth et al. 2001) by either suppressing or enhancing biotic and abiotic responses in plants (Agrawal et al. 2003; Zaid and Mohammad 2018). MeJ plays a well-established role in plant salinity stress tolerance. MeJ triggered tolerance to salt stress in genotypes of *Oryza sativa* by maintaining increased MeJ biosynthesis and mediating a tolerance trade-off with ABA (Kang et al. 2005). In a recent study, Golezani and Abriz (2018) applied foliar sprays of MeJ along with SA in soybean plants under salt stress. Both MeJ and SA stimulated H^+-ATPase activity and influenced nutrient uptake to improve salt stress tolerance. In wheat seedling, exogenous 2.0 mM MeJ treatment for 3 days alleviated salt stress by boosting the activities and transcript levels of antioxidant battery proteins, viz. CAT, SOD, and APX, and also enhanced the reduced glutathione (GSH) contents, photosynthetic pigments and carotenoids and decreased peroxidation of lipids and biosynthesis of ROS (Qiu et al. 2014). Walia et al. (2007) observed the physiological responses and transcriptome effects in barley under salt stress conditions. MeJ-mediated expression of ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO) activase, apoplastic invertase, and arginine decarboxylase conferred salt stress tolerance. In wheat plants, *allene oxide cyclase* gene was responsible to engineer salt stress tolerance *via* signalling of MeJ (Zhao et al. 2014). Crosstalk between MeJ and ABA mediates improved salt stress tolerance in tomato plants (Orsini et al. 2010). Thus, from the above discussion, it is clear that MeJ controls various processes in plants to improve salt stress tolerance.

4.3.6 Melatonin

Mel (N-acetyl-5-methoxytryptamine) is an active harmless endogenous biologically active molecule which is biosynthesized in endocrine glands of animals and in various plant parts (Wang et al. 2017; Sharif et al. 2018; Arnao and Hernandez-Ruiz 2018). Mel is regarded as an important secondary messenger which has been evidenced to regulate various abiotic and biotic pressures in plants (Yin et al. 2013; Zhang et al. 2015; Xu et al. 2016; Wei et al. 2018; Nawaz et al. 2018). In recent decades, Mel has gathered special attention as a signalling molecule in plant responses to drought, salt, high temperature, and chemical stresses, as it is implicated to control various developmental processes; hence, the exploration of its role and underlying mechanisms in plants has emerged a rapidly growing field in recent years. Various evidences indicated that abiotic pressures could trigger the biosynthesis of Mel endogenously in plants. Studies have indicated the beneficial role of Mel in salinity stress tolerance (Li et al. 2012; Shi et al. 2015; Chen et al. 2017; Yu et al. 2018). Nevertheless, the exogenous supply of Mel improves plants' growth and development during salt-challenged environments. In watermelon plants, different doses of Mel (50, 150, and 500 μM) pretreatment improve photosynthesis and redox homoeostasis under salinity stress (Li et al. 2017). Salinity stress (NaCl 300 mM) affected photosynthesis and increased biosynthesis of ROS and membrane damage. However, plants receiving Mel pretreatment alleviated the adverse effects of NaCl-induced decrease in photosynthetic rate and oxidative damage. Mel-mediated protection of photosynthesis was related to inhibition of stomatal closure and improvement in absorption of light energy and electron transport rate in photosystem II. Mel also enhanced antioxidant enzyme activities which led to maintained redox homoeostasis under salinity stress conditions (Jiang et al. 2016; Li et al. 2017). In *Arabidopsis*, endogenous Mel trigger signalling of ROS and control ROS-mediated Na^+ extrusion to improve salt stress tolerance (Chen et al. 2017). In *Malus hupehensis*, Li et al. (2012) worked out the role of Mel in countering high-salinity (100 mM NaCl)-induced alterations. Mel reduced the growth inhibition and improved photosynthetic capacity and reduced oxidative damage induced by salt stress. Furthermore, Mel also controlled the ion-channel-related expression of genes, viz. *MdNHX1* and *MdAKT1,* under salinity stress. Gene expression was greatly upregulated, which in turn regulated the maintenance of ion homoeostasis leading to improved tolerance to salt stress (Li et al. 2012). Application of Mel

(1 μM) enhanced salt tolerance in maize (Jiang et al. 2016). Mel-mediated improvement during salinity stress conditions was attributed to the increased capacity of photosynthesis, enhanced antioxidative ability, and regulation of ion homoeostasis (Li et al. 2012; Jiang et al. 2016). In yet recent study, Yu et al. (2018) applied Mel simultaneously to the leaves and roots of *Ipomoea batatas* under 150 mM NaCl stress. They carried out electrophysiological experiments and lipidomic profiling, which confirmed that Mel significantly lowered NaCl-mediated effects. Mel also upregulated the gene expression related to salt-induced lipid breakdown, β-oxidation of fatty acids, and energy turnover. These findings clearly indicated that Mel improves tolerance to salt stress conditions by regulating various morpho-physiological and biochemical processes in plants.

4.4 Conclusions and Future Prospects

Exogenous application of PGRs like SA, NO, BRs, ABA, MeJ, and Mel could alleviate the adverse impacts of salinity stress in plants. The tolerance trade-off mediated by various PGRs via regulating a range of cellular, biochemical, and molecular processes results in improved salt stress tolerance in plants. Various biosynthetic pathways modulated by PGRs set a basis for generation of genetically engineered transgenic with elevated salt stress tolerance for improving the productivity of various crop plants in the coming decades in salt-challenged habitats. Thus, it is evident that for tailoring plant responses in salt stress conditions in relation to yield and quality of crop plants, the tolerance trade-off of different PGRs could positively modulate salt stress tolerance.

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Impact of Plant-Microbe Interactions on Plant Metabolism Under Saline Environment

5

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Abstract

Soil salinity is a significant abiotic stress causing a remarkable decrease in crop production. The plant-microbe interactions can affect the metabolism of plant under saline stress causing changes in major processes like germination, growth, and nutrient imbalance. Changes also can be seen in root and shoot induction hormone levels during growth. There can be difficulty in uptake of water due to reduced osmotic potential due to osmotic dormancy. Plant growth-promoting rhizobacteria (PGPR) improve and enhance plant growth and yield. Production of different compounds results in increased root length and number of root tips. Many actinomycetes are also components of rhizosphere microbial communities and play a major role in plant growth. Presence of ACC deaminase under saline condition causes increase in chlorophyll content and seed germination in okra plants. These microorganisms also help in reducing ethylene stress. This chapter also discusses about a new study on induced systemic tolerance to salt stress with *Arabidopsis* using *Bacillus subtilis*. The plant-associated mycobiota that include various mycorrhizal fungi and other fungi play a major role in stress tolerance. The tolerance of plant to salt stress is found to be positively correlated with anti-oxidant enzyme activity. These antioxidant enzymes and ROS scavengers are responsible for direct or indirect removal of ROS. Soil salinity is a major factor that limits the productivity of crops, it has been proposed that half of the land in the world that is suitable for growth of crops will be salinized by 2050, and improved strategies are being developed which include different plant-microbe interactions that can assist plant growth under salt stress. Thus, the aim of the present chapter is to focus on the impact of plant-microbe interactions on plant metabolism under saline environment and also on the involved mechanisms.

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5.1 Introduction

Many essential and beneficial nutrients are required for plants like other living organisms. They also have great roles in plant metabolism, biochemistry, growth, and development. Copper is a major constituent of proteins which takes part in electron transfer and oxygen transport, whereas manganese is the main nutrient for many plant functions such as transport of electrons during photosynthesis and forming of riboflavin, carotene, and ascorbic acid. Zinc helps in achieving root development and auxin production (Osman 2013; El-Ramady et al. 2015; Mitra 2017; Luo et al. 2015; Secco et al. 2017; Zhang et al. 2017).

Soil salinity is one of the great threats facing the global food security. This is caused by natural or anthropogenic factors and has been recognized as a serious challenge in land cultivation worldwide in arid and semiarid regions. Thus, soil salinity is a significant abiotic stress causing a remarkable decrease in the crop production under such soil conditions (Hasanuzzaman et al. 2013). Concerning damage caused by salinization, it could lead to the disruption or alteration of the natural biochemical (Decock et al. 2015), biological (Smith et al. 2015), hydrological (Keesstra et al. 2012), and erosional (Berendse et al. 2015) cycles. It has been reported that salt-affected soils constitute nearly 10% of the total global land (about 1 billion ha) including saline soils (Shahid et al. 2013) and several mechanisms for plant salt tolerance (Almutairi 2016).

Plant-microbe interactions can affect plant metabolism in various ways under saline condition, different temperatures for different periods of time and also different pH of saline solutions. The behaviour of plant and microbes under different conditions may vary separately. The physiological and molecular responses of plants against stress can bring a change in metabolism. As known under saline conditions, plants will have to activate various biochemical and physiological mechanisms to cope with the stress resulting from saline conditions. This response can also be due to an impact of plant-microbe interaction causing different mechanisms to get activated (Parida et al. 2004). Thus, the aim of the present chapter is to focus on the impact of plant-microbe interactions on plant metabolism under saline environment and also on the involved mechanisms.

5.2 Plant Metabolism

Plant metabolism is the complex of chemical and physical events of photosynthesis, respiration and the synthesis and degradation of organic compounds. Photosynthesis is one of the main processes of plants and produces substrates for respiration, and few starting organic compounds are used as building blocks for biosynthesis of amino acids, carbohydrates, nucleic acids, proteins, lipids and natural products. In addition, plant secondary metabolism produces products that help and assist the plant in development and growth, but these are not required for plant survival. Plant-microbe interactions involve adaptations between the interacting partners. The development and growth of plant depend on coordinated assimilate production, distribution and allocation. The identification of microbial factors and their host targets involved in regulation of plant primary metabolism is to increase crop yield. Plant metabolism is driven by autotrophic nature of plants. It exhibits a flexibility that is not seen in other higher organisms.

5.3 Impact of Salinity on Plants

Salt stress is one of the primary abiotic stresses that cause major changes in the metabolism of the plants. Normally this happens in plants that are grown in semiarid regions of the world. There are two effects that salt stress causes on plants reducing its growth rate: one is salt can cause reduction of water uptake from soil to the plants due to the fact that it causes change in osmotic pressure (Khan and Weber 2008). Moreover, too much salt can cause damages to the cells that transpire in leaves through the ion toxicity effect hence killing the cell in the long run. Salt stress causes changes in major processes like germination, growth, nutrient imbalance and changes in yield (Khan and Rizvi 1994). Therefore, salt stress is something that should be looked at and remedies must be discovered due to the ever-changing environment. Based on the sensitivity to salt concentrations in the soil, plants can be divided into two types: halophytes, i.e. ones that are highly tolerant to salt and grow in these conditions, and glycophytes, which are plants that are highly sensitive to the high saline conditions in the soil and don’t survive saline environment.

Germination is the process where the plant grows from the seed; changes to this process cause major changes to the plant morphology and its yield. Salt stress causes several effects on the germinating seed like reduced water uptake due to the changes in the osmotic pressure and changes in the nucleic acid metabolism, and furthermore it has effects on protein metabolism that can cause a wide range of changes to the plant itself during growth. It primarily affects plants like rice (*Oryza* species) (Xu et al. 2011), corn (*Zea mays* species) (Carpici et al. 2009; Khodarahmpour et al. 2012) and other major crops. Salt stress also varies based on the way plants are cultivated and the climatic regions where plants are being cultivated. It is found that germination has a negative correlation with the increase in salinity in the soil on a typical salt-sensitive plant, resulting in reduced germination or delayed germination (Bordi 2010; Fig. 5.1). In an experiment it was found that there is a high reduction in size of various parts of the plant like plumule, and there is moderate reduction in the vigour of the plant (Khodarahmpour et al. 2012).

Salt stress also causes major changes to the root and shoot induction hormone during the growth of the plants. It was found that there are major changes to the plant hormone induction during the initial growth phase of the plant under salt stress, but later it remained constant, whereas in some other plants, there was a

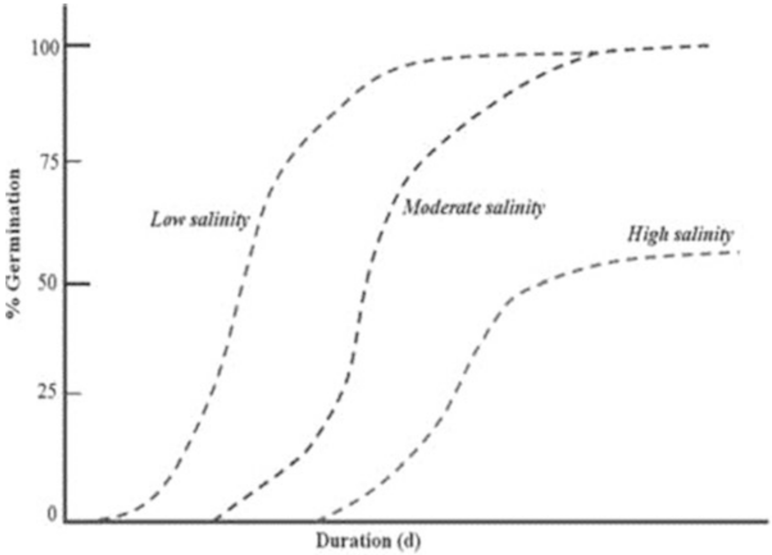

Fig. 5.1 Relationship between rate of germination and time after sowing at different salinity levels. (Adapted from Lauchli and Grattan 2007)

major increase in leaf Abscisic Acid (ABA) induction on increase in salt stress. Also, it was found that cytokinin levels in the leaves were found to decrease on increase in salt concentration. This is due to the induction of stomatal resistance by plants under high-stress conditions. It was also found that stomatal resistance is caused due to the increased levels of xylem ABA. It was theorized that ABA was known to have been necessary to coordinate the stomatal function and maintain the water budget in the xylem system under salt stress by stomata opening. ABA is also responsible for the signalling of plant cells during the invent of salt stress; this helps in regulation of genes encoding key enzymes that form the ABA, and it also upregulates the ethylene production that is a hormone known to cause senescence in plants.

The presence of high salt concentrations in soil also causes competitions for minerals with the plants hence reducing the essential mineral uptake by the plant. The presence of increased Na^+ and Cl^- ions causes reduced uptake of minerals like magnesium, phosphorus, nitrogen and calcium which are known to be essential for the metabolism of the plant (Zhu 2001). Increased presence of Na^+ ions is known to affect the integrity of cell membranes due to membrane's polar nature (Kurth et al. 1986). The decreased presence of Ca^{2+} and Mg^{2+} ions in the plant cells causes functional weakness in the cell membranes and reduced chlorophyll content in the mesophyll cells of the plant (Parida et al. 2004).Often plants are known to accumulate the salts in the shoot tissues when grown in the saline environment, and hence the presence of high concentration of Cl^- ions causes plant growth reduction due to toxicity. There has been evidence that NaCl stress also causes reduction in photosynthesis ability as they reduce the stomatal conductance, reducing the transport of energetic ions between the cells for metabolism (Tavakkoli et al. 2011; Fig. 5.2).

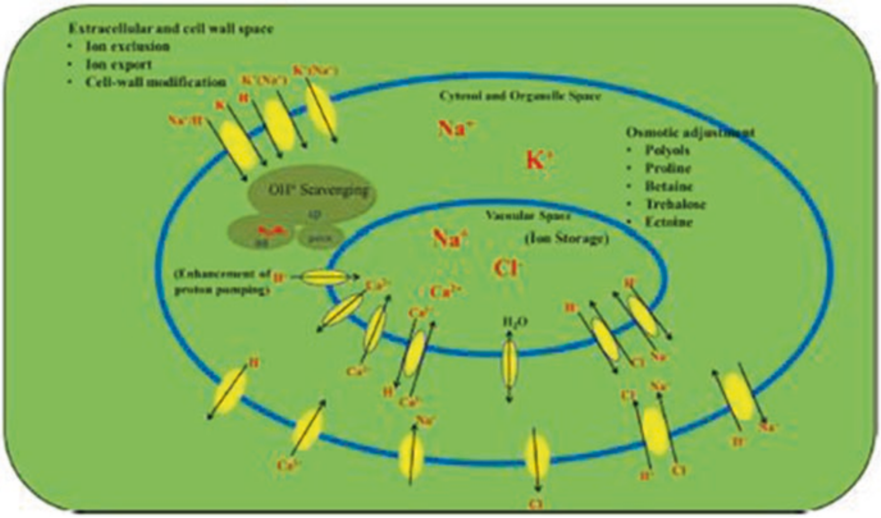

Fig. 5.2 The schematic presentation of a cell includes three separate parts that are defined by the extracellular space: cytosolic space and vacuolar space

However, there are many methods that plants take to curb the high salt toxicity, one of which is through restriction of mechanism of salt uptake and control long-distance transport of Na^+ and Cl^- ions.

5.3.1 Physiological and Chemical Changes on Fruits Under Salt Stress

It is well known from the previous section that increasing salt concentration can cause massive changes in plant characteristics. We found that there are changes in germination pattern, increased ionic influence by Na^+ and Cl^- ions in the metabolism pathways, decreased photosynthesis behaviour and weakening of plant cell membrane. In tomatoes under salt stress, it was found that there is reduction in germination time but increase in the time taken for it to grow into a complete plant. Also, it was found that the yield of tomatoes reduced with increasing salt concentration when the salinity was increased from 2.5 to 3.0 dS in the irrigated water. Also it was found that there is decrease in fruit weight and the number of fruits produced by a single plant hence reducing the overall weight of the produce. Even it was found that there is significant decrease in the root growth at high salt concentrations (4.0–6.0 dS), and it also reduces the ability to take in water due to the changes in osmotic potential. But overall at moderate salt concentrations, it is found that tomatoes have increased fruit taste as sugars and acids increase at the cost of reduction in shelf life (Cuartero and Fernandez-munoz 1998).

In eggplants it was found that increase in salt concentration caused difficulty in uptake of water due to reduced osmotic potential causing osmotic dormancy. But in contrast it was found that the eggplants showed an increase in starch storage. This further caused decrease in yield when it crosses a threshold of 1.5 and 6.7 dS of Na^+ and Cl^- in the soil in different eggplant species (Ali et al. 2010). Also increased Cl^- content in the leaves caused creation of reactive oxygen species that ultimately destroyed the leaves of the crop (Wang et al. 2008). In strawberries it was found that there was increase in production of antioxidant enzymes such as catalase and superoxide dismutase to prevent damage caused by the increase in ROS species during salt stress. But on addition of NO, exogenously activity of antioxidant enzymes increased, and hence the yield of strawberries started to increase overall (Jamali et al. 2014). There are also reports that there is significant increase in phenolic products (10% increase) during high salt stress (above 40 mM) (Keutgen and Pawelzik 2007). It was also found that salt-stressed strawberries tend to have less sweet taste due to the decrease in production of sugars, organic acids and other essential compounds. Moreover, in grapes it was found that the plant tends to have inhibition of shoot growth due to reduced intake of water. It also affected the metabolic transcripts causing decrease in production of sugars like glucose, malate and proline compared to when they were in water stress (Cramer et al. 2007). As salt-stressed grapevines are known to have decreased pigments, the photosynthetic ability also decreases, but on the use of Si on the grapevines, there is increase in production of sugar and starch hinting that Si protects the plant during salt stress (Lin et al. 2016). Rice is often found to be resistant to salt stress because of the presence of ion exclusion and osmotic tolerance, but in turn this increases signals that cause reduction in shoot growth and the upregulation of antioxidant enzymes.

5.4 Plant Growth-Promoting Rhizobacteria (PGPR)

PGPR are a group of beneficial free-living bacteria that live in the soil and improve plant growth and yield. PGPR are characterized by their ability to compete with other microorganisms to survive and multiply and promote plant growth. Rhizobacteria mostly belong to Gram-negative rods with less abundance in Gram-positive cocci and rods (Bhattacharyya and Jha 2012). Some examples of PGPR are *Arthrobacter*, *Agrobacterium*, *Azospirillum*, *Allorhizobium*, *Azorhizobium*, *Azotobacter*, *Burkholderia*, *Bradyrhizobium*, *Bacillus*, *Caulobacter*, *Erwinia*, *Flavobacterium*, *Micrococcus*, *Mesorhizobium*, *Rhizobium* and *Pseudomonas* (Bhattacharyya and Jha 2012).

Classification of PGPR based on their functionality is as follows: (1) biopesticides (able to control diseases, by the production of antifungal and antibiotics metabolites), (2) biofertilizers (increase in nutrient availability to plant), (3) rhizoremediators (degradation of soil contaminants) and (4) phytostimulators (promotion of plant growth, through phytohormones) (Somers et al. 2004). Moreover, many actinomycetes are also components of rhizosphere microbial communities and play a role in promotion of plant growth. Among them a few have shown enormous potential as biocontrol agents (*Streptomyces* spp., *Micromonospora* sp. and

Thermobifida sp.) against different root fungal pathogens (Bhattacharyya and Jha 2012; Franco-Correa et al. 2010). Production of indole acetic acid, gibberellins and some unknown determinants by PGPR results in increased root length, root surface area and number of root tips, leading to an enhanced uptake of nutrients, thereby improving plant health under stress conditions (Egamberdieva and Kucharova 2009).

5.4.1 Plant Growth in the Presence of ACC Deaminase Under Saline Condition

Increased salt concentrations reduce seed germination as well as root growth in dicotyledonous plants. Decreased germination in the presence of saline conditions is due to fact that the osmotic potential of the growth medium increases resulting in more energy requirement for water absorption by seeds. Seed germination of okra was decreased at a higher rate with increasing level of salinity. By maintaining the low ethylene levels and high ROS scavenging enzymes, the ACC deaminase containing PGPR increased the chlorophyll content, seed germination and growth of okra plants under saline stress. Ethylene is considered as a stress hormone as it is synthesized at a rapid rate under stress (Stearns and Glick 2003). High concentrations of this stress hormone often hinder plant growth due to reduced root development (Belimov et al. 2001; Saravanakumar and Samiyappan 2007). It also decreases seed germination. ACC deaminase synthesizing microorganisms can cleave the ACC to α-ketobutyrate and ammonia; this results in decrease in ethylene stress in plants (Sun et al. 2009). A study conducted by Sheikh Hasna Habib et al. with *B. megaterium* UPMR2 and *Enterobacter* sp. UPMR18 which contained ACC deaminase activity demonstrated induced salt tolerance and subsequently improved the growth of okra plants under salt stress.

Wild-type *P. putida* UW4 and *Gigaspora rosea* BEG9 containing ACC when inoculated with cucumber plants under 72 mM salt stress (Gamalero et al. 2010) showed significantly higher biomass compared to those which were ACC deaminase deficient. Red pepper seedlings which were inoculated with ACC deaminase-containing salt-tolerant bacteria reduced 57% stress ethylene production and produced similar amounts of biomass as to those in no salt treatment control plant (Siddikee et al. 2011). A study conducted by Mayak et al. (2004) showed that the ethylene content in tomato seedlings exposed to high salt was reduced by application of *Achromobacter piechaudii*, due to its production of ACC deaminase, thus increasing the tomato seedling growth by as much as 66% in the presence of high salt contents.

Presence of ACC deaminase increases the leaf chlorophyll concentration. Chlorophyll is destroyed due to extreme amounts of salts, ions (Na^+ and Cl^-) or reactive oxygen species (ROS) disturbing the cellular metabolism and resulting in the degeneration of cell organelles in the leaf tissue (Hassine and Lutts 2010). On the other hand, the inoculated salt-stressed okra plants showed higher chlorophyll content and dark green leaves due to the presence of ACC deaminase-containing PGPR isolates that maintain the photosynthetic efficiency of plants by decreasing ethylene biosynthesis.

Salinity stress leads to the formation of ROS, namely, superoxide (O_2^-), singlet oxygen (O_2), hydroxyl (OH^-), and hydrogen peroxide (H_2O_2), which cause severe damage to cell structures by exerting oxidation of cell membranes, a process known as oxidative stress (Apel and Hirt 2004). However, a defensive system known as the antioxidant enzyme system is also activated under stress conditions. This system comprises several ROS-scavenging enzymes such as superoxide dismutase (SOD), peroxidase (POD), glutathione reductase (GR), monohydroascorbate reductase (MDHAR), ascorbate peroxidase (APX) and catalase (CAT). These antioxidant enzymes can remove the free radicals produced during abiotic stress conditions in the cell (Abbas et al. 2013). The okra plants inoculated with ACC deaminase-containing PGPR exhibited significant elevation of antioxidant enzyme activities (APX, CAT and SOD) compared to non-inoculated plants under saline conditions, thus confirming that PGPR-inoculated plants were adaptable to saline conditions by eliminating ROS through APX, CAT and SOD activities.

5.4.2 Induced Systemic Tolerance to Salt Stress

Induced systemic tolerance (IST) to salt stress was also noted in a new study with *Arabidopsis* using *Bacillus subtilis* GB03, a species that has previously been used as a commercial biological control agent. Interestingly, few volatile organic compounds (VOCs) that are emitted from *B. subtilis* GB03 (Ryu et al. 2004) (Fig. 5.3) are bacterial determinants involved in IST. Among the 600 *Arabidopsis* genes isolated by transcriptome analysis, transcriptional expression of HIGH-AFFINITY K^+ TRANSPORTER 1 (HKT1), which controls Na^+ import in roots, was decreased. HKT1 has been shown to regulate Na^+ and K^+ levels differentially, depending on the plant tissue. Exposure of an athkt1 mutant to bacterial VOCs not solely resulted in typical salt stress phenotypes, such as stunting, but also led to the inhibition of seedling growth. Transcriptional validation showed that bacterial VOCs downregulated HKT1 expression in roots, but upregulated it in shoot tissues, thereby orchestrating lower Na^+ levels in the whole plant. Furthermore, there’s no distinction in IST to salt stress within the Na^+-export mutant salt excessively sensitive3 (sos3), suggesting that HKT1 functions in shoots to retrieve Na^+ from the xylem, thereby facilitating shoot-to-root Na^+ recirculation. Overall, plant perception of bacterial VOC causes a tissue-specific regulation of HKT1 that controls Na^+ homeostasis under salt stress.

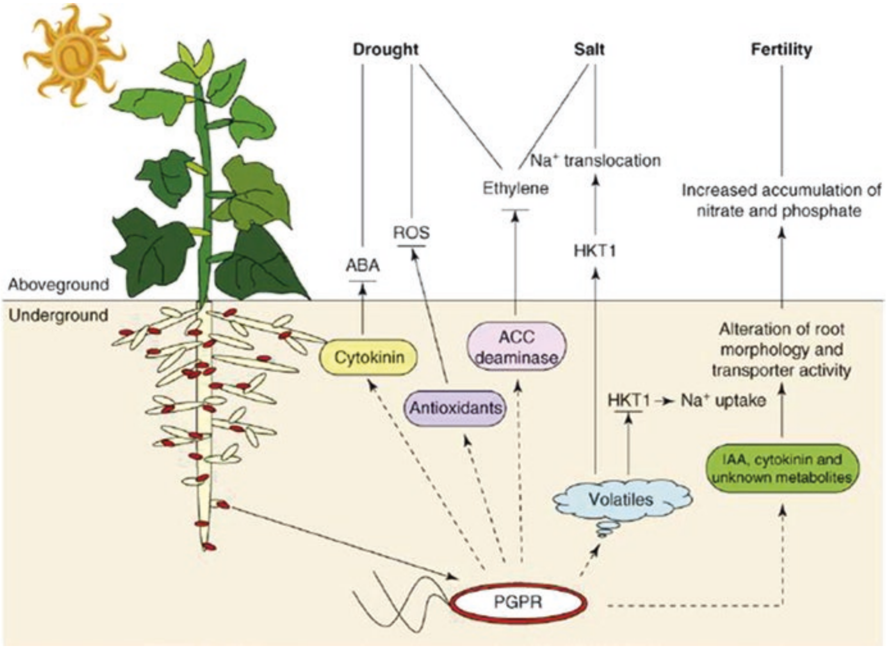

Fig. 5.3 IST elicited by PGPR against drought, salt and fertility stresses underground (root) and aboveground (shoot). Broken arrows indicate bioactive compounds secreted by PGPR; solid arrows indicate plant compounds affected by bacterial components. Some PGPR strains, indicated in red on the plant roots, produce cytokinin and antioxidants such as catalase, which results in ABA accumulation and ROS degradation, respectively. Degradation of the ethylene precursor ACC by bacterial ACC deaminase releases plant stress and rescues normal plant growth under drought and salt stresses. The volatiles emitted by PGPR downregulate hkt1 expression in roots but upregulate it in shoot tissues, orchestrating lower Na^+ levels and recirculation of Na^+ in the whole plant under high salt conditions. Production by PGPR of IAA or unknown determinants can increase root length, root surface area and the number of root tips, leading to enhanced uptake of nitrate and phosphorous. Abbreviations: *ABA* abscisic acid, *ACC* 1-aminocyclopropane-1-carboxylate, *HKT1* high-affinity K^+ transporter 1, *IAA* indole acetic acid, *IST* induced systemic tolerance, *PGPR* plant growth-promoting rhizobacteria, *ROS* reactive oxygen species. (Adapted from Jungwook et al. 2009)

5.5 Fungal Interactions with Plants and Salt Stresses

Association of fungi with plants has been known since a long time now, for example, mycorrhiza, which was one of the earliest, well-described and extensively studied symbiosis system. These plant-associated mycobiota consist of various members that include mycorrhizal fungi as well as a number of ascomycetes and non-mycorrhizal basidiomycetes (Qin et al. 2017). Playing a major role in plant nutrition and stress tolerance, these organisms are significant for plant growth. Fungal associations could be endophytic or epiphytic depending on whether the fungi lived within the plant or it grew attached to the plant. Fungal endophytes have the potential to induce certain plant stress genes and other biomolecules like reactive oxygen

Table 5.1 Role of plant growth-promoting bacteria in salinity stress alleviation in plants (Mayak et al. 2004; Nadeem et al. 2007; Palaniyandi et al. 2014)

Plant growth-promoting bacterial species	Crop plant	Effect
Achromobacter piechaudii	Tomato (*Lycopersicon esculentum*)	Reduced levels of ethylene and improved plant growth
Azospirillum	Maize (*Zea mays*)	Restricted Na^+ uptake and increased K^+ and Ca_2^+ uptake along with increased nitrate reductase and nitrogenase activity
Pseudomonas syringae, *P. fluorescens* and *Enterobacter aerogenes*	Maize (*Zea mays*)	ACC deaminase activity
Bacillus subtilis	*Arabidopsis thaliana*	Tissue-specific regulation of sodium transporter HKT1
Rhizobium sp. *Pseudomonas* sp.	Mung bean (*Vigna radiata* L.)	IAA production and ACC deaminase activity
Streptomyces sp. *strain* PGPA39	'Micro-tom' tomato	ACC deaminase activity and IAA production and phosphate solubilization
P. Pseudoalcaligenes *B. pumilus*	Salt-sensitive rice GJ-17	Reduce lipid peroxidation and superoxide dismutase activity

species (ROS) scavengers that can improve plant growth under abiotic stress conditions (Lata et al. 2018). The tolerance of plant to salt stress is found to be positively correlated with the activity of antioxidant enzymes (Gupta and Huang 2014). These antioxidant enzymes and ROS scavengers are responsible for the direct or indirect removal of ROS.

P. indica, a root endophyte, provides tolerance against saline stress in rice plants. PiHOG1, a stress regulator MAP kinase, plays a significant role in the regulation of genes involved in salinity tolerance of the rice plant (Jogawat et al. 2016). *Trichoderma* spp. are known potential plant growth promoters (Hermosa et al. 2012). They reduce the effect of plant pathogens present in the soil and hence reduce the intensity of plant diseases. They increase plant growth potential inducing resistance and tolerance to abiotic stresses and pathogens by interacting with plant roots. In many plant species, they also induce tolerance to saline conditions. Some of the important plant species that showed improved stress tolerance and growth are maize (*Zea mays*), wheat (*Triticum aestivum*), rice (*Oryza sativa L.*), *Arabidopsis*, tomatoes and many more (Zhang et al. 2016; Yasmeen and Siddiqui 2017). *Trichoderma longibrachiatum* T6 increased the tolerance and growth of wheat in high saline conditions (Zhang et al. 2016). The relative water content of the roots increased in the presence of T6 in saline conditions. The chlorophyll content of leaves decreases in saline conditions due to the presence of ROS, which leads to retarded growth. The addition of T6 to these wheat plants resulted in reversing the decrease in chlorophyll content by inhibiting the action of ROS. Proline is a nitrogen source that has a significant role in repair and promotes growth in abiotic stress conditions; it acts as an osmolyte and reduces the uptake of toxic compounds by reducing the osmotic potential of the cell. The level of proline biosynthesis is upregulated in the presence of T6 both in saline or nonsaline conditions. The stress in plants is indicated by the overproduction of ROS. They are the main reasons for salt-induced damage to macromolecules and plant structures. In order to fight these conditions, many enzymes such as SOD, POD and CAT, which provide a protective mechanism against these ROS and detoxify the system, are synthesized in plants. In saline conditions, these enzymes are usually produced in large quantities. The addition of T6 further increased the activity and expression of these enzymes. Some of the other *Trichoderma* spp. that showed similar results are *T. virens*, *T. harzianum* and *T. atroviride*. Arbuscular mycorrhizal fungi (AMF) like *Glomus intraradices* when colonized with various plant species like tomato, maize and pepper plants showed greater growth at many salinity levels compared to non-mycorrhizal plants. Salt stress leads to loss in membrane stability; hence, maintenance of membrane stability is one way to tolerate this stress conditions. AMF symbiosis improves the cell membrane stability; this was suggested by comparing the membrane permeability of stressed pepper plants inoculated with AMF which was less permeable than that of non-inoculated pepper plants (Beltranco et al. 2013). In coastal conditions, *F. culmorum* was seen to exhibit habitat-specific salt tolerance (Rodriguez et al. 2008). FcRed1 strain decreased the extent of salt stress on plants (tomato and rice). The plants that survived had both FcRed1 and mycorrhizae, while the one that failed to survive had only the mycorrhizae. This indicated that the synergic effect of both produced the salt tolerance. *F. culmorum* exhibits habitat-specific salt tolerance because another strain Fc18 did not induce salt tolerance even though the growth rate of Fc18 was higher than FcRed1 in saline conditions (in vitro). This is because of the insufficient colonization capacity of Fc18 as compared to FcRed1 resulting in higher quantities of FcRed1 compared to Fc18 in saline conditions.

Productivity of crops is limited by various factors; one such factor is soil salinity. It has been proposed that half of the land in the world that is suitable for growth of crops will be salinized by the year 2050 (Jamil et al. 2011). It is hence essential to develop strategies that can assist plant growth under high salt stress. Though the development of genetically modified salt-tolerant plants is possible, it is not cost efficient and can be time consuming. Instead, the inoculation of fungi, which can be easily performed, helps in inducing salt-tolerant plant varieties. Fungi have shown to be very effective partners of plants in this case, overcoming salt stress through various mechanisms that have been briefly discussed above.

5.6 Conclusions and Future Prospects

Salinity is a major concern for decline in crop production in many countries due to increasing climate change. This primarily occurs due to the decrease in photosynthetic and water absorbing capability of plants in highly saline soils. It also affects the regulation of ABA in certain plants which leads to decrease in water mismanagement and decrease in the rate of growth. We also understand that certain plant-friendly microbes can help the plants to survive and thrive in highly salty soil conditions like the beneficial rhizobacteria. Therefore, we can also work on using genetically engineered microorganisms to help the plant to survive the increasing salt-prone soil environment. Use of new techniques to identify the plant-promoting characteristics and find the right inoculation practices can help in discovering new methods of using this symbiotic relationship to the next level. Also investing in these technologies that help in increasing the survivability of the microbes and the efficiency is also important for successful beneficial relationship. Thus, the uses of beneficial microorganisms are known to be less aggressive as compared to the use of chemical fertilizers which makes it a sustainable farming practice.

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Plant Survival and Tolerance Under High Salinity: Primary and Secondary Cell Wall-Sensing Mechanism

6

Amrina Shafi and Insha Zahoor

Abstract

Soil salinity is a widespread abiotic stress constraint which poses a threat to agricultural production, as it severely inhibits plant growth and development. One of the most prompt responses that plants trigger towards adaptations to saline environments is differential regulation of growth and expression of key genes, which results in growth either away from adverse conditions or towards more favourable conditions. The dynamic changes occur in growth and development of the plant, a process in which plant cell walls play important roles. Therefore, it is likely that cell wall changes are required for differential growth responses to changing environmental conditions. Cell wall constantly sensing environmental conditions and communicating with other parts of the cell, which adjust and communicate in a feedback loop to affect conditions at the wall, by triggering a cascade of reactions leading to tolerance. Thus, cell wall plays an active role in response to exogenous stimuli and constitutes a step forward in demarcating the complex pathways regulating the response of plants to salt stress. Understanding how salinity stress factors influence primary and secondary cell wall growth and mechanisms that improve plants' ability to produce biomass can provide crucial information to cope with the need for increased crop production under the escalating pressures of a growing world population and global climate change. The present chapter focuses on identifying and understanding the functions of the cell

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wall-related genes, metabolites, and signalling molecules that initiate and carry out primary and secondary cell wall synthesis during salinity stress.

Keywords
Antioxidants · Biomass accumulation · Metabolites · Salinity stress · Transcription factors

6.1 Introduction

Environmental variations have a direct influence on plant growth, yield, and biomass production (Wang and Frei 2011; Dolferus 2014). An array of physiological, morphological, and biochemical strategies have been accomplished by plants to evade or tolerate stress conditions (Jin et al. 2010; Wu et al. 2014; Munné-Bosch et al. 2013). Reactive oxygen species (ROS) regulation is changed in response to stress; regarded as lethal consequences and also attributed as major signalling molecules at low concentration, thus participating in the adjustment of the cellular machinery in response to salt stresses (Wrzaczek et al. 2013; Shabala and Munns 2012). Plants require a relatively large network of genes for reactive oxygen species (ROS) homoeostasis and to use these potentially toxic molecules as signals (Mittler et al. 2012; Yokawa and Baluška 2014). Among these ROS molecules, H_2O_2 is relatively more stable and is also able to diffuse freely among cellular compartments and between cells (Wrzaczek et al. 2013; Gill and Tuteja 2010). H_2O_2 at optimum concentration has been demonstrated to act as an essential signalling molecule, regulating many developmental and physiological processes under abiotic stresses (Miller et al. 2010). Plant biomass is largely made up of plant cell walls, which provide the major sustainable resource for many human products and the first line of defence against any kind of abiotic stress, and this resistance arises from the ultrastructural properties of the plant cell wall (Somerville et al. 2010).

Plants typically contain two different types of cell walls: a primary wall that surrounds all growing cells and a secondary wall that provides support to specialized cells (McFarlane et al. 2014). Cellulose biosynthesis produces the main load-bearing elements of primary and secondary plant cell walls and represents major sinks for photosynthesis products followed by hemicellulose, lignin, and pectin (Demura and Ye 2010). The massive deposition of cellulose and hemicelluloses inside primary walls gives secondary walls their characteristic thickness (Liepman et al. 2010). Cell wall not only determines cell shape and architecture but also helps in plant stress sensing and signal transduction (Seifert and Blaukopf 2010; Liepman et al. 2010). During stress conditions, the cell wall has to maintain its integrity while also having to meet different functional requirements (Deinlein et al. 2014). The structure and composition of cell wall can be modified by various abiotic stress factors, and changes may affect the biomechanical properties, e.g. through chemical modifications of the cell wall components, e.g. in *Coffea arabica* L. leaves, salt stress caused changes in pectic fractions, which led to the stiffening of the cell wall resulting in decreasing of its permeability for salt (De Lima et al. 2014). Salt stress induced lignification in roots of soybean and tolerance (Neves et al. 2010; An et al.

2014). Similarly, in petioles of an aspen hybrid and maize (Uddin et al. 2013), increased rigidity of the cell wall formed a barrier for salt entrance (Muszyńska et al. 2014). Overexpression of enzyme responsible for pectin degradation (the β subunit of polygalacturonase 1) led to increased sensitivity of transgenic rice plants to cold, drought, and salt stresses (Liu et al. 2014). Expression of the genes encoding cell wall proteins, lignin, and cellulose synthesis was induced in *Arabidopsis* and potato by salt stress (Shafi et al. 2014, 2015a, b, 2017, 2018).

The signals that control the developmental switch from primary to secondary wall synthesis in higher plants are not known (Seifert and Blaukopf 2010). This transition is characterized by termination of synthesis of polymers unique to the primary cell wall accompanied by enhanced rates of cellulose deposition and induction of synthesis of specific secondary wall matrix polysaccharides and lignin. Recent evidence of regulatory systems that link sensing and signalling of environmental conditions and the intracellular redox status have shed light on interfaces of stress and energy signalling (Xiong et al. 2015). Recent research advances suggest and support a regulatory role of ROS in the crosstalks of stress-triggered cell wall modifications (Shafi et al. 2015a, b, 2017, 2018). H_2O_2 has been proposed to be involved in the induction of secondary cell wall cellulose biosynthesis and dimerization of cellulose synthase subunits (Shafi et al. 2018). Recently, H_2O_2 has also been found to play a role in increasing cell expansion and root diameter in rice by enhanced accumulation of pectin (Xiong et al. 2015). Thus, plants are continually challenged to recognize and respond to environmental stresses so as to avoid adverse effects on growth and development. Acclimation of plants to changes in their environment requires a state of cellular homoeostasis achieved by a delicate balance between multiple pathways that reside in different cellular compartments, and among that, cell wall modification is the first defence against any kind of hostile conditions. This coordination may, however, be disrupted during different stresses, especially when the cell or the entire plant is exposed to a rapid decrease in water potential, or when additional environmental parameters are involved. Thus, the present chapter focuses on identifying and understanding the functions of the cell wall-related genes, metabolites, and signalling molecules that initiate and carry out primary and secondary cell wall synthesis during salinity stress.

6.2 Primary and Secondary Cell Wall with Its Components

Plant cell walls are dynamic structures described as a complex of carbohydrate and protein. Cell walls have been classified as primary or secondary; the primary wall is laid down during cell division and expansion, and the material deposited on the primary wall once growth has ceased is termed the secondary wall (Richet et al. 2011). Primary cell walls are composed of polysaccharides, smaller proportions of glycoproteins, and, in some specialized cell types, various noncarbohydrate substances such as lignin, suberin, cutin, cutan, or silica. Wall polysaccharides fall into three categories: pectins, hemicelluloses, and cellulose (Krzeslowska 2011). Pectins and hemicelluloses are components of the wall "matrix", within which are embedded the skeletal, cellulosic microfibrils. Polysaccharides represent up to 95% of cell wall mass, whereas cell wall proteins (CWPs) only account for 5–10% (Krzeslowska 2011; Sasidharan et al. 2011). Models of cell wall structure describe the arrangement of their components into dense interwoven networks of polysaccharides and proteins (Zagorchev et al. 2014). Cellulose microfibrils and hemicelluloses constitute a network; another one is formed by structural proteins, e.g. extensions, and both are embedded in a pectin matrix. Three types of CWPs can be distinguished on the basis of their interactions with cell wall components (Zagorchev et al. 2014; Zhao et al. 2013).

The deposition of a thick lignified secondary cell wall only occurs once cells have attained their final shape and size. The plant cell wall is a dynamic and complex structure whose functional integrity is constantly being monitored and maintained during development and interactions with the environment. Most plant cell wall models now view these structures as a type of polymer liquid crystal (PLC) where cellulose fibril networks are embedded in non-cellulosic polysaccharide matrixes (hemicelluloses and pectin), composed with lignin, and structural proteins (Peaucelle et al. 2012). Cellulose is the dominant polysaccharide in plant cell walls and often described as “the most abundant biopolymer on earth”. These cellulose microfibrils are then cross-linked by hemicelluloses/pectin matrixes during cell growing (Peaucelle et al. 2012). Principal components of secondary cell walls are cellulose, hemicelluloses, and lignin, which are all essential for maintaining the normal strength of secondary walls as a reduction in any one of them by genetic mutations leads to a defect in secondary cell walls and a concomitant decrease in secondary wall strength (Vanholme et al. 2010). Cellulose microfibrils together with hemicelluloses form the main load-bearing network in secondary cell walls. Lignin is the second most abundant plant biopolymer mainly present in the secondary walls of tracheary elements, and fibres in wood, a major component of the vascular plant cell wall, provide mechanical support for plants to stand upright and enable xylems to withstand the negative pressure generated during water transport. Lignin also sequesters atmospheric carbon in its tissues and thereby plays an important role in the carbon cycle. Lignification consequently transformed phenylpropanoid metabolism into a major sink for carbon in plants, eclipsed only by cellulose, such that it has now been estimated to represent as much as 30% of the total biomass produced in the biosphere (Wang et al. 2013). Lignin is a heterogeneous phenolic polymer (Fig. 6.1) largely composed of three major types of monomers (monolignols), as *p*-coumaryl, coniferyl, and sinapyl alcohols (Wang et al. 2013). During lignin deposition, monolignols are synthesized in the cytoplasm, translocated to the apoplast, and polymerized into lignin (Fig. 6.1). Cross-linking of the monolignols in the wall is brought about by laccases and/or peroxidases (Wang et al. 2013).

6.3 Salt Stress-Induced Changes in Cellulose Biosynthesis

During abiotic stress, ultrastructural properties of plant cell wall give protection and act as the first line of defence against any kind of detrimental effects on plants (Moura et al. 2010). Recent reviews have explored how abiotic cues modify

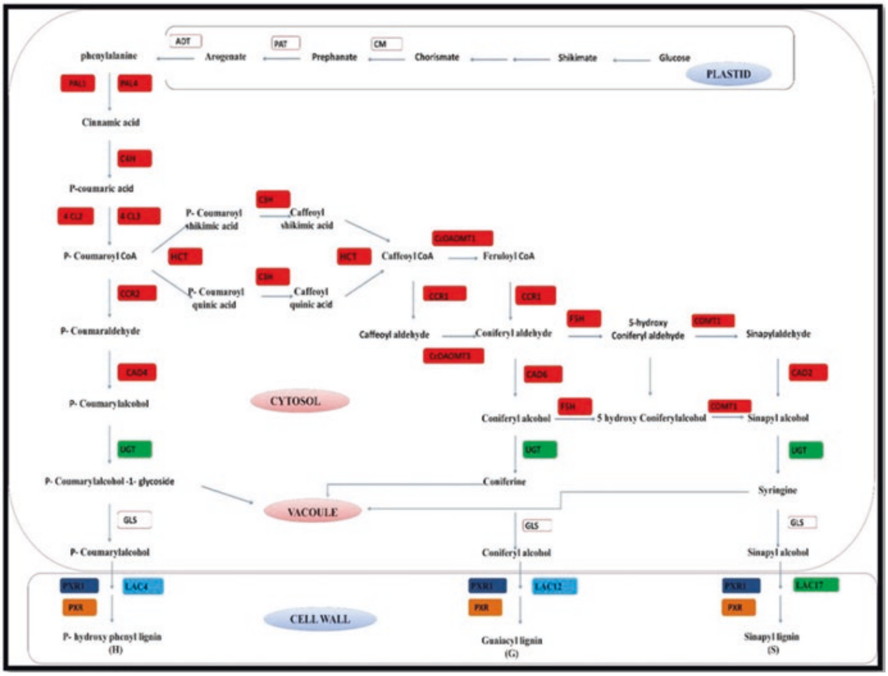

Fig. 6.1 Overview of lignin biosynthesis pathway. Each arrow shows a reaction in the pathway, and next to each arrow is the name of the enzyme that catalyses the associated reaction. Abbreviations are listed as per pathway. *CM* chorismate mutase, *PAT* prephenate aminotransferase, *AGT* arogenate dehydratase, *PAL* phenylalanine ammonia lyase, *C4H* cinnamate 4-hydroxylase, *4CL* coumarate:CoA ligase, *CCR* cinnamoyl-CoA reductase, *CAD* cinnamyl alcohol dehydrogenase, *HCT* hydroxycinnamoyl-CoA transferase, *C3H* *p*-coumarate 3-hydroxylase, *F5H* ferulate 5-hydroxylase, *COMT* caffeic acid *O*-methyltransferase, *UGT* UDP-glucosyltransferase, *LAC* laccases, *PXR* peroxidases, *CCoAOMT* caffeoyl-CoA 3-O-methyltransferase, *H lignin* p-hydroxyphenyl lignin, *G lignin* guaiacyl lignin monomers, *S lignin* syringyl lignin monomer

cellulose biosynthesis (Wang et al. 2016), how expansins and peroxidases influence wall stiffness during stress (Tenhaken 2014), and how modifications in non-cellulosic polysaccharides such as xyloglucan accompany stress responses (Le Gall et al. 2015). In the plant cell wall, cellulose constitutes the major component of both primary and secondary cell walls and represents a major sink for photosynthesis products (Sasidharan et al. 2011). In Arabidopsis tissues, cellulose is an important component of cell wall changes required for directional cell expansion in response to changing abiotic conditions. Other cell wall components, such as lignin (Moura et al. 2010) and matrix polysaccharides (Tenhaken 2014), are clearly altered under biotic and abiotic stresses. Cellulose microfibrils not only determine cell shape and patterns of development, but are also involved in stress response (Wang et al. 2016). Salinity for a prolonged period in barley roots can regulate various genes involved in cellulose biosynthesis (Ueda et al. 2007). A similar effect has been reported in the cell wall of petioles of an aspen hybrid, where the increased rigidity acts as a barrier for salt permeation (Muszyńska et al. 2014). To survive under abiotic stress, improvement of secondary cell wall thickening by increased deposition of hemicellulose and cellulose (Wang et al. 2016) and through enhanced lignin content (Shafi et al. 2015a, 2017) in the cell wall has been reported previously. In *Arabidopsis*, several CesA genes showed implication in salt stress response (Heyndrickx et al. 2014), but the detailed experimental investigation is still lacking.

Saline conditions can affect many aspects of plant growth. Generally, salt stress can be subdivided into two pathways: an early-occurring osmotic stress response, which is due to salt outside of cells, and an ionic stress response due to the accumulation of ions (e.g. Na^+) inside cells. In *Arabidopsis*, cellulose synthase (CesA) genes have been implicated in salt stress responses via bioinformatic analyses of gene regulatory networks and gene ontology annotations (Heyndrickx and Vandepoele 2012). Plants display shoot growth inhibition during the first phase of salt stress, partly due to a loss of cell wall extensibility. In maize, reduced cell wall extensibility was related to the formation and accumulation of diferulic acid cross-links in the cell (Uddin et al. 2013). Changes in cell wall structure appear to be a common feature of the response to salt stress. For instance, in coffee plants grown with 150 mM NaCl during 25 days, the palisade and spongy parenchyma exhibited thinner cells, which might be related to decreasing water content in leaf cells (De Lima et al. 2014). Additionally, changes to osmotic conditions can alter cell expansion, especially of the roots, resulting in directional plant growth towards more favourable water conditions or away from high salt conditions (Galvan-Ampudia and Testerink 2011). Both the orientation of cellulose microfibrils and the composition of the cell wall are important factors that govern the direction of cell expansion (Peaucelle et al. 2015), implying that cellulose may be directly or indirectly regulated by water availability. Furthermore, *KOB* transcript was specifically downregulated in the root epidermis and cortex in response to salt treatment. KORRIGAN (KOR) is endoglucanase that directly interacted with CesAs at the plasma membrane and potentially in intracellular compartments (Liebminger et al. 2013; Vain et al. 2014). Several transcription factors are involved in cellulose biosynthesis under stress conditions (Fig. 6.2), NAC family (SND2/3) master switches which activate NAC downstream effectors (MYB20/42/43/52), which directly affect (MYB54/69/103/KNAT7) cellulose, xylan, and pectin biosynthesis genes (Fig. 6.2).

6.4 Salt Stress-Induced Changes in Lignin Biosynthesis

To cope with many of the abiotic and biotic stresses, a series of specialized metabolic pathways, often referred to as secondary metabolism, evolved in early land plants, among which phenylpropanoid metabolism was probably one of the most critical (Moura et al. 2010; Cabane et al. 2013). Cell wall lignification occurs as a common stress response and provides structural rigidity and durability to plant tissues (Moura et al. 2010). Lignin is important for the plant's response to environmental stress, for reinforcement during secondary cell wall formation and for long-distance water transport. Lignin induction has been correlated with abiotic

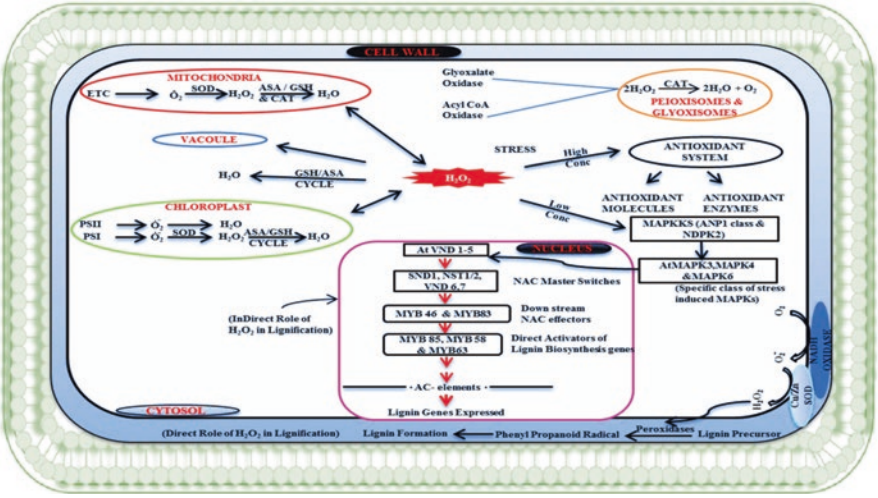

Fig. 6.2 Transcriptional network regulating secondary wall biosynthesis and lignification. In this network, SND1, NST1/2, VND6/7, and its close homologs are master switches of the secondary wall biosynthetic programme. MYB46/83 and its function downstream of the NAC master switches. MYB58/63/85 directly activate the expression of lignin biosynthetic genes through binding to the AC elements. Similarly, SND2/3 activate MYB20/42/43/52, which in turn activate downstream effectors MYB54/69/103 and KNAT7, and finally activate cellulose, xylan, and pectin biosynthesis genes

stresses as well as mechanical injuries in a large number of different plant species (Moura et al. 2010). Lignification therefore can be seen as a remarkably versatile tool allowing plants' considerable flexibility in dealing with environmental stresses as diverse as mechanical challenges.

Under salt stress, thicker wall protects cell interior more efficiently against ion absorption. Salinity stress has been associated with higher deposition of lignin in vascular tissues and/or xylem development (Shafi et al. 2015a, b, 2017). Cell wall lignification strengthens cell wall for long-distance water transport and provides structural rigidity and robustness to conducting tissues (Kim and Barbara 2008). Recent findings have indicated that salinity stress is associated with altered anatomical beneficial changes, such as higher deposition of lignin in vascular tissues in salt-treated *Arabidopsis* (Shafi et al. 2015a, b) and in the xylem elements of potato plants (Shafi et al. 2017) which facilitated water flow and maintained the structural integrity of vascular tissues during salt stress. Under salt stress, lignification finds it substantial role at the anatomical and ultrastructural level, where it enables long-distance water transport and sustain structural reinforcement of the vascular tissue. Recently, it was shown that lignin serves as a major component of the casparian strip in *Arabidopsis* thaliana roots and also prevents ion diffusion in the root endodermis (Naseer et al. 2012).

Specifically, at the cellular level, it has been shown that salt stress affects the cell wall by both a decrease in cell expansion (Iraki et al. 1989) and an increase in the polymerization of monolignols of the root (Cruz et al. 1992). Under salt stress, the thicker the wall, the more efficiently the cell interior is protected against ion absorption. In general, cell walls suffer lignification during plant stress (Christensen et al. 1998). Salinity stress has been associated with a greater deposition of lignin in vascular tissues and/or xylem development (Liu et al. 2014). Coordinated morphological, histochemical, and biochemical analyses have been reinforcing the role of salt stress on lignification and related processes in cell walls. Long-term salinization inhibited the elongation of primary root growth by inducing a hardening of cell walls in the growing tips of maize (Neumann et al. 1994). Saline stress retarded primary xylem differentiation and induced increased development of secondary xylem in soybean roots (Hilal et al. 1998). Finally, Sanchez-Aguayo et al. (2004) observed the relative abundance of lignified tracheary elements within vascular bundles in salt-treated tomato plants. Presumably, this increase in the number of lignified tracheary elements under salt stress may enhance the cell-to-cell pathway for water transport and greater selectivity and ion uptake.

Cell wall lignification of protoxylem and metaxylem vessels may contribute to the structural integrity of xylem vessels (Smart and Amrheim 1985) during the adaptation of bean plants to salt stress, through the formation of lignin-polysaccharide linkages (Ohnishi et al. 1992). This may be of great importance, since xylem vessels are subjected to the tensile and compressive forces of the transpiration stream, which may be severely affected in salt-stressed glycophytic plants in order to maintain transpiration rates of similar magnitude to those found in control plants (Horie et al. 2012). Salt stress has been shown to impact secondary cell wall formation and structure, as revealed by an altered lignin biosynthesis. Salt treatment increased root lignification and the number of lignified vessels (Neves et al. 2010). Many enzymes involved in the lignin biosynthesis pathway were altered upon salt treatment, e.g. a caffeic acid 3-O-methyltransferase (COMT) in alfalfa and a peroxidase in tomato (TPX1), which is involved in the synthesis of lignin and changed their expression pattern in response to various environmental stresses (Quiroga et al. 2000; Shafi et al. 2015a). Lignin subunit composition and overall quantity may vary under the influence of environmental stress (Wang et al. 2013; Shafi et al. 2015a).

6.4.1 MYB and NAC Family Transcription Factors Regulate Lignin Biosynthesis

Cellulose, hemicelluloses, and lignin constitute secondary cell wall components; their biosynthesis occurs by coordinated expression of various genes and transcription factors (SND1, NSTs, and VNDs) (Zhong et al. 2007). High salinity usually induces the expression of secondary cell wall genes and transcription factors which regulate their expression, among which MYB and NAC transcription factors (Shafi et al. 2015a, 2017, 2018) are recognized to be involved in various tolerance and adaptation. Secondary cell wall deposition in plants is an important and dynamic phenomenon and several transcription factors involved in its regulation have been identified in previous studies (Zhong et al. 2007). A number of transcription factors belonging to NAC and MYB family (Fig. 6.3) have been discovered to be master switches, activating the secondary cell wall biosynthetic programme in *Arabidopsis* (Zhou et al. 2009; Shafi et al. 2015a) (Fig. 6.3). It is presumed that increased H_2O_2 levels could be perceived directly by TFs that orchestrate downstream cascade (Miller et al. 2010). It is found that stress leads to the production of H_2O_2, which serves as a secondary messenger and relay the signal to MAP kinases (MEKK1, MPK3, MPK4 and MPK6) and TFs, such as NAC, ZAT, WRKY, DREB, bZIP, and MYB (Zhong et al. 2008). Deletion analyses in the promoters of PAL and 4CL genes identified cis-acting (AC) elements critical for their expression in vascular tissues (Levya et al. 1992). It was shown that MYB protein was able to bind to the AC elements (Fig. 6.3) and turn on the expression of a reporter gene driven by the PAL and 4CL1 promoters (Zhou et al. 2009). These MYBs are part of SND1/NST1-mediated transcription network involved in regulation of secondary cell wall biosynthesis in fibres and vessels, where they bind to the AC elements in the promoters

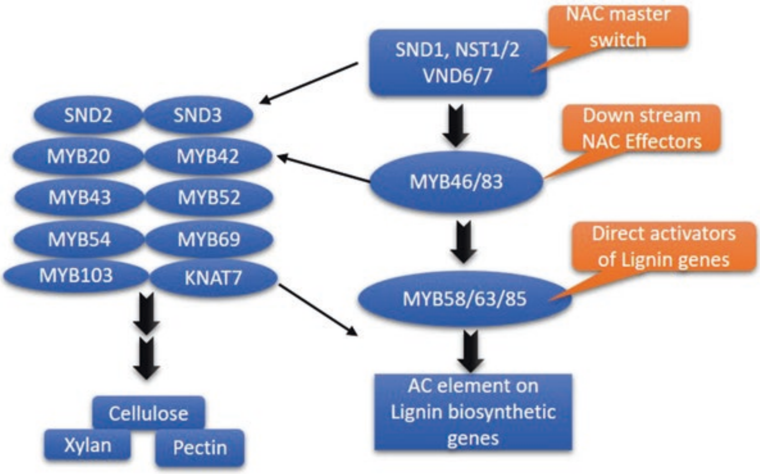

Fig. 6.3 Model depicting H_2O_2-mediated lignin biosynthesis in higher plants. Overexpressing SOD and APX antioxidant genes, H_2O_2 accumulates in the cytosol during stress conditions by the action of SOD in various cell compartments. At high concentration, H_2O_2 activates the antioxidant system which optimizes its concentration. At low concentration, H_2O_2 acts as a messenger activating a specific class of stress-induced MAPKs which phosphorylate NAC TFs including SND1, NST1/2, and VND6/7 that in turn activate a nexus of intermediate TFs, mostly MYBs. These intermediate TFs finally activate MYB TFs that directly bind to the promoters of target cell wall biosynthetic genes and activate them. In this signalling cascade, SND1, NST1/2, and VND6/7 act as NAC master switch controlling downstream NAC effectors (MYB46 and MYB83) which further regulate MYB85, MYB58, and MYB63 TFs which act as direct activators of lignin biosynthesis genes. In addition, H_2O_2 generated by the action of cell wall-derived NADH oxidases and CuZn-SOD acts as a direct substrate for peroxidases-mediated monolignol polymerization. Abbreviations are listed as, H_2O_2 hydrogen peroxide, *SOD* superoxide dismutase, *APX* Ascorbate peroxidase, *CAT* catalase; ASA, ascorbate; GSH, glutathione; VND, vascular-related NAC domain; SND, secondary wall-associated NAC domain protein; NST, NAC secondary wall thickening promoting factor

and serve as common means for the coordinated regulation of genes in the entire monolignol biosynthesis pathway (Zhong et al. 2008; Zhou et al. 2009). Three NAC TFs, NST1, NST2, and NST3, were also shown to regulate the entire secondary cell wall programme in *Arabidopsis* (Zhong et al. 2008). The SND1 and NST1 (SND3) act as master switches activating downstream target MYB46 and MYB83 which are positive regulators of lignin biosynthesis in fibres and vessels (Zhong et al. 2007). The NST homologs VND6 and VND7, which are involved in xylem vessel formation, were able to upregulate MYB46 directly, suggesting that they also regulate the lignin pathway (Mitsuda et al. 2007). This MYB46 in turn acts as another key regulator (Fig. 6.3) of the entire secondary wall biosynthetic programme (Zhong et al. 2007). H_2O_2 also acts as a potent activator of a MAPK cascade in various tissues (Desikan et al. 1999) and constitutive activation of an H_2O_2-responsive MAPK-mediated cross-tolerance to various environmental stresses by activating stress-responsive genes (Kovtun et al. 2000).

6.4.2 Role of Antioxidant Enzymes in Lignification Under Stress

Biosynthesis of lignin is a complex process and regulated usually by ROS (Krasensky and Jonak 2012). Recent research indicates that the enhanced lignification of plant tissues by ROS is due to the imbalance between ROS and its scavenging systems during senescence or under stress conditions (Liu et al. 2010). During stress conditions, ROS are produced, and to scavenge ROS molecules, plants have an antioxidant defence system, which includes antioxidant enzymes (catalase, superoxide dismutase, ascorbate peroxidases, glutathione reductase, and cell wall-bound peroxidases). Activities of antioxidant enzymes increase in several crop species (Liu et al. 2010) under salt stress. In this situation, the antioxidant system could protect the plant against reactive oxygen species generated by NaCl. Among these enzymes are the cell wall-bound peroxidases (POD) often considered being most directly involved in lignifications (Almagro et al. 2009). In addition, Gulen et al. (2006) and Talano et al. (2006) showed a significant increase in a basic isoperoxidase associated with the lingo-suberization of cell walls in the leaves of strawberry and in tomato hairy roots, respectively. Lignin biosynthesis is accompanied by an increase in the activities of cell wall-bound POD, and this process involves oxidative coupling, dependent on H_2O_2, which causes a rapid cross-linking of the cell wall polymers (Almagro et al. 2009).

The "cytosolic" CuZn-SOD which is localized in the cytosol near the vacuole, the nucleus, and the apoplastic region (Ogawa et al. 1996) and the localizing site of CuZn-SOD in the apoplastic region of spinach leaf tissues correspond to that of the accumulation of lignin. In spinach hypocotyl "cytosolic" CuZn-SOD is localized in vascular tissues where lignification and the generation of superoxide take place. Because hydrogen peroxide is required for lignification via the peroxidase-catalysed reaction, the CuZn-SOD in the apoplast appears to function in the biosynthesis of lignin by causing rapid disproportionation of the superoxide anion radical prior to its interaction with cellular components and peroxidase. Thus, the association of

CuZn-SOD with the nucleus indicates it has a role in preventing fatal mutation caused by reactive species of oxygen. Ogawa et al. (1997) have shown the generating enzyme of superoxide anions in the vascular tissue of spinach hypocotyls and assessed the contribution of CuZn-SOD and NAD(P)H oxidase to the formation of hydrogen peroxide using inhibitors of CuZn-SOD, guaiacol peroxidase, and NAD(P)H oxidase. They concluded that CuZn-SOD is essential to lignification since it supplies hydrogen peroxide and protects the peroxidase from inactivation by superoxide. The involvement of SOD and H_2O_2 in cell wall lignification was further supported by several groups independently (Kim and Barbara 2008). Recently, transgenic plants overexpressing CuZn-SOD (*PaSOD*) gene isolated from a high altitude plant, *Potentilla atrosanguinea,* had enhanced lignification in the vascular system and exhibited tolerance against salt stress (Gill and Tuteja 2010; Shafi et al. 2015a, 2014). This study suggested that there is a link between oxidative stress and enhanced secondary cell wall formation. However, the signal transduction pathway of cell wall lignifications under salt stress is not fully understood.

6.4.3 Signalling Role of Hydrogen Peroxide (H_2O_2) in Lignification Under Salt Stress

Active oxygen species may also have a positive role in plant growth and development. H_2O_2 is the most stable and probable candidate for ROS-mediated signal transduction; it has the ability to cross the membrane barrier and reach the site of action due to its uncharged nature (Golldack et al. 2014). H_2O_2 at lower concentration participates in signalling pathways, and at higher concentration, H_2O_2 oxidizes cellular components and can initiate chain reactions triggering cellular apoptosis (Vellosillo et al. 2010). H_2O_2 can regulate plant development, stress adaptation, and programmed cell death (Klaus and Heribert 2004). H_2O_2 as a signalling molecule also regulates the expression of genes encoding antioxidants, cell rescue/defence proteins, and signalling proteins such as kinase, phosphatase, and transcription factors (Neill et al. 2002). Low levels of ROS molecules also have beneficial roles which include cell wall polymerization. The plant cell wall is important not only for maintaining cell shape, but it also responds to endogenous and environmental cues through the release of signalling molecules, such as H_2O_2. However, the primary function of reactive oxygen species (ROS) production in the plant cell wall is to modify cell wall components by processes of cell wall stiffening/softening, which, in the last instance, control plant growth and morphogenesis. In response to cell wall damage (CWD), putatively compensatory responses such as lignin production are initiated (Shafi et al. 2014, 2015a, 2018). H_2O_2 is produced on the outer face of the plasma membrane of both differentiating (living) thin-walled xylem cells and particular (non-lignifying) xylem parenchyma cells. From the production sites, it diffuses to the differentiating (secondary cell wall-forming) and differentiated lignifying xylem vessels.

The delicate balance between ROS production and scavenging that allows this duality in function to exist in plants is thought to be orchestrated by a large network of genes termed the "ROS gene network", which includes more than 152 genes in *Arabidopsis* tightly regulating ROS production and scavenging (Mittler et al. 2004). Among ROS, H_2O_2 was viewed mainly as a toxic cellular metabolite, but it became evident that it has multiple roles in plants. It can function as a signalling molecule that mediates responses to various stimuli in plants (Neill et al. 2002). H_2O_2 induces polymerization of different subunits of lignin (4-hydroxy cinnamaldehyde, coniferyl alcohol, and sinapyl alcohol), leading to a complete lignin deposition (Donnini et al. 2011). In addition, a microarray study showed that the expression of 1–2% of genes was altered in H_2O_2-treated *Arabidopsis* cultures and particular genes encoding antioxidant enzymes were upregulated (Desikan et al. 2001). Production of H_2O_2 in the lignified xylem elements has been reported in several plant species, which was presumed to be a strong trigger initiating the peroxidase-dependent oxidation of cinnamyl alcohol to lignins (Almagro et al. 2009). As far as H_2O_2 production is concerned, a very interesting theory has been suggested in which NADH-driven reversal of the general peroxidase reaction is supposed to provide the required hydrogen peroxide for lignification and wall stiffening (Gross et al. 1977). The available evidence indicates that amino oxidases present in the apoplast may have a physiological role within the cell wall and can account for the H_2O_2 needed in the peroxidatic coupling of lignin subunits and in-wall stiffening. A possible role for H_2O_2 in the signalling for APX induction in plants has been described by different authors (Faize et al. 2011). Low levels of H_2O_2 help in cell wall polymerization and generation of secondary messengers for signal transduction pathways (Neill et al. 2002).

6.5 Transgenic Approaches for Enhancing Cell Wall Biosynthesis and Stress Tolerance

Conventional plant breeding approaches through which beneficial traits are transferred into elite varieties generate stress-tolerant varieties (Ashraf 2010; Varshney et al. 2011). However, as salinity tolerance is a multigenic trait, such approaches have only limited success, which can explain the absence of commercially available salt-tolerant crops. Therefore, biotechnological approaches including genetic engineering seem to be more beneficial alternatives. Engineering crops with enhanced salt stress tolerance traits are one of the most important challenges for modern agriculture. Several studies have shown an increase in lignin and cellulose content or change in its composition under stress conditions (Moura et al. 2010).

- Overexpression of antioxidant genes (SOD and APX) in *Arabidopsis* transgenic plants conferred a strong phenotype with enhanced inflorescences, lignification, and strong salt tolerance, indicating the key role of antioxidant genes in response to salt stress (Shafi et al. 2014, 2015a).
- Transgenic approaches have also shown the role of several peroxidases in lignin synthesis. In tomato overexpression of peroxidase "TPX1" significantly increased the lignin content in transgenic tomato plants (Mansouri et al. 1999).

- It was also reported that both lignin content and composition were affected by downregulation of certain class III peroxidases (Blee et al. 2003).
- The presence of an extra copy of SOD helps in efficient scavenging of superoxide molecules along with lignification of the vascular system of transgenic potato, leading to efficient uptake of water and metabolites and better survival of plant under stress condition (Shafi et al. 2017).
- Previous studies have shown that ectopic deposition of lignin is governed by overexpression of NAC and MYB transcription factors (Zhou et al. 2009).
- In another study performed on transgenic *Arabidopsis*, overexpressing antioxidant genes showed higher cellulose accumulation in the secondary cell wall, highlighting the key role of cellulose biosynthesis in salt tolerance (Shafi et al. 2018).
- In physic nut roots (*Jatropha curcas*), expansion genes were both upregulated and downregulated, while *XET* genes were upregulated during different periods of salt exposure at 100 mM NaCl (Zhang et al. 2014).
- Transgenic plants have also been used to validate the role of candidate genes potentially involved in cell wall production/modification and abiotic stress. Transgenic *Arabidopsis* and tomato (Choi et al. 2011) lines expressing the *Capsicum XTH* showed increased salt tolerance and had longer roots than control plants lacking the transgene, suggesting a role for wall flexibility in alleviating stress responses.
- In maize root tissues, multiple cell wall-related genes were found to be differentially expressed under salt stress (Li et al. 2014), including *ZmXET1*. *ZmXET1* is thought to be involved in cell wall extension as it is capable of hydrolysing and rejoining xyloglucan molecules.
- Li et al. (2014) identified different expansins, *ZmEXPA1, ZmEXPA3, ZmEXPA5, ZmEXPB1, and ZmEXPB2*, being upregulated when plants were subjected to increased salinity and, therefore, are possibly involved in mediating resistance against salinity-related toxicity.
- Overexpression of *OsBURP16* was found to increase the amount of polygalacturonase (PG), an enzyme which hydrolyses pectin, and change the composition of the plant cell wall (Liu et al. 2014).

6.6 Conclusion and Future Prospects

In conclusion, the cell wall plays an important role in salt tolerance, especially in the detection of salt stress. An increasingly important global challenge is to utilize our land and water resources as efficiently as possible to sustain our growing population. Plants are essential primary producers, and the growth ranges of different plants are often defined by abiotic factors, such as temperature, light, and soil conditions. The analysis of a large set of data shows that the plant response is highly complex and that shows the difficulty of identifying a common pattern of stress response in cell wall architecture that could enable adaptation to abiotic stress. Therefore, understanding plant growth and cell expansion under different abiotic conditions is a crucial future challenge. Recent research advances have elucidated a molecular cellular signalling network for the understanding of how plants control and regulate adaptation to the abiotic stresses salinity. Essentially, molecular signalling components in plant adaptation to environmental adversity have been connected to hub transcription factors (NAC, MYB), MAPK pathways, and ROS pathways. Prominently, it is expected that further and prospective advances in the network modelling of cellular abiotic stress signalling will provide new and efficient strategies for improving environmental tolerance in crops. A better understanding of these tolerance mechanisms can be used to breed crops with improved yield performance under salinity stress. Over the last two decades, research made on *Arabidopsis* and a few crops shed light on several aspects of the molecular mechanisms controlling the salt stress tolerance. However, many challenges still lie ahead before successfully improving crop yield under saline conditions. Taken together, these results show the need to undertake large-scale analyses, using multidisciplinary approaches, to unravel the consequences of stress on the cell wall. This will help identify the key components that could be targeted to improve biomass production under stress conditions.

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Field Application of Rhizobial Inoculants in Enhancing Faba Bean Production in Acidic Soils: An Innovative Strategy to Improve Crop Productivity

7

Alemayehu Getahun, Diriba Muleta, Fassil Assefa,
and Solomon Kiros

Abstract

Faba bean is the most vital legume crop in Ethiopia, but abiotic stresses primarily soil acidity are an obstacle for its production. Soil acidity disturbs and potentially limits nitrogen-fixing symbiosis. The interruption of nitrogen fixation and faba bean rhizobia interaction as a result of soil acidity leads to decreasing crop production. Sole dependence on chemical fertilizers for agricultural growth would mean further loss in soil quality and increased environmental damage. Rhizobial species show off sizable metabolic abilities to mitigate abiotic and biotic stresses, and mechanisms in stress tolerance are advancing fast, offering a strong foundation for the choice and engineering of rhizobia and legume hosts with better tolerance to soil acidity accordingly. The vast efforts to pick bioinoculants that can restore nitrogen under acid-affected soils are producing competitive crop yields. The main challenge of using single-type bioinoculant in field application can lead to variable and inconsistent outcomes. Co-inoculation of compatible microbes with organic farming which does not involve use of synthetic pesticides and chemical fertilizers is an imperative element in sustainable agriculture. Therefore, the present chapter focuses on the field application of faba bean rhizobial inoculants in acidic soils as a promising potential input in organic farming system. Moreover, the mechanism of N_2 fixation and plant growth promotion systems under severe salt, drought, acidity, temperature, and heavy metal stresses is also highlighted.

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7.1 Introduction

Legumes play a predominant role in lowering poverty and improving human health and nutrition while restoring ecosystem services (Jaiswal et al. 2018). Among legume crops, faba bean (*Vicia faba* L.) is one of the important food legumes to satisfy human protein needs in the era of escalating price of animals' meat. Strong demand for food requires unique efforts for ample production. Today's agriculture is characterized by soil fertility loss, local weather alternates, and multiplied pest attacks (Mabrouk et al. 2018). Population growth and reduction in land on hand for cultivation with endless environmental constraints (extremely low/high temperature, soil acidity, salinity, drought, flooding, and heavy metals) are principal threats for agricultural sustainability (Shahbaz and Ashraf 2013). Agriculture is the predominant monetary endeavor in the growing countries including Ethiopia appealing over 50% of the population with low crop productivity owing to environmental stresses which include soil acidity (Alori et al. 2017). Moreover, increasing demand for food production with shrinking land resources is a principal venture to agricultural sustainability (Owen et al. 2015). Currently, the use of rhizobacteria and rhizobia has been of great help in combating the aforementioned stressful factors that limit the overall performance of faba bean crop (Kabata et al. 2017). The need of more sustainable agriculture practices, specifically the reduction of chemical fertilizers, highlights the significance of biological nitrogen fixation by symbiotic legume-rhizobia associations (Adesemoye and Kloepper 2009).

Faba bean is one of the earliest domesticated food legumes and occupies nearly 3.2 million hectares worldwide and is a major component of a daily diet in Ethiopia (Abebe et al. 2014). Due to its high dietary value and capability to grow over a wide range of climatic and soil conditions, cultivation of faba bean is appropriate for sustainable agriculture in many marginal areas (Youseif et al. 2017). Faba beans are fast growing and high-yielding crop with remarkably significant economic and ecological roles (Sahile et al. 2008). It has been considered as a meat extender or substitute due to its high protein content material (20–41%) (Crépon et al. 2010). In Ethiopia faba bean is grown mainly by using subsistence farming, during the cool season (June–September) (Weldua et al. 2012). In 2017–2018 cropping season, faba bean occupies about 437,106 hectares of land with an annual countrywide production of 1,016,068.2 tons, with a productivity of 2.11 tons ha^{-1} (Damtie Mengistie 2018). However, the productivity of the crops under smallholder farmers is not greater than 1.89 t ha^{-1} (Demissie et al. 2016). The low yields per hectare have been related with susceptibility of the plants to biotic and abiotic stresses (Sahile et al. 2009). The main cereal crop production constraint in most sub-Saharan Africa nations is the loss of soil fertility (Nyoki and Ndakidemi 2016). Soil acidity is a primary issue to crop production in the world. Declining soil fertility due to soil acidity is the most determinant factor. Annual nutrient deficit is also estimated to be −41 kg N, −6kg P, and

−26 kg K ha^{-1} (Kebede and Yamoah 2009). In addition, the highland location is a place that receives excessive rainfall and characterized as acidic soil which causes high phosphorus fixation, leaching nitrogen and potassium.

Modern farming practices have an effect on our world, via land degradation, nutrient runoff, soil erosion, water pollution, and destruction of traditional knowledge systems (Patil et al. 2013). When the soil contains a significant proportion of non-nodulating or ineffective nitrogen-fixing rhizobia as a result of soil acidity, it leads to decreasing crop production. Sole dependence on chemical fertilizers for crop cultivation would mean further loss in soil quality and extremely increased environmental damage. The chemical provides an instantaneous impact on crop production and however creates long-term ill outcomes on environment (Das and Singh 2014).

As a result of un-affordability of the cost of chemical fertilizers and their long-term negative ecological impact, there is a great need to explore biological means to improve soil health and crop productivity. Organic farming has emerged as an important priority area to realize safe and healthy food and continuing agriculture protecting environmental damage (Mahdi et al. 2010). These can be achieved by reducing(avoiding) the use of synthetic fertilizers, pesticides, growth regulators, and livestock feed additives (Das and Singh 2014). Organic farming comprises biofertilizers and organic amendments which are ready to use phytobeneficial live microorganisms and biowastes. The use of microbial inoculants has a prominent role in enhancing productivity due to their ability to release the bound nutrients in most organic matter at required times for crop utilization (Parr et al. 1994). Recently studies have shown that several plant species require microbial associations for stress tolerance and survival (de Zelicourt et al. 2013). Plant growth-promoting rhizobacteria (PGPR) and rhizobia can improve the growth of crops under abiotic stresses for sustainable agriculture (Egamberdieva and Kucharova 2009). The beneficial roles of PGPR and rhizobia have been achieved via nutrient availability and uptake and support the health of soil and plants (Alori et al. 2017). Field experimental results from acidic soils of Western Kenya showed that rhizobial inoculation increased nodule number and weight per plant and inoculation accounted for 58.91% and 78.95% in increased fixed N levels (Ogega et al. 2018). Generally, agricultural practices in the past 60 years have been dependent on external inputs (pesticides and fertilizers). All these environmental- and health-related problems in the world inspired the use of eco-friendly bio-tools to maximize growth and productivity of legumes by alleviating different stresses. Therefore, the present chapter focuses on the field application of faba bean rhizobial inoculants in acidic soils as a promising potential input in organic farming system. Moreover, the mechanism of N_2 fixation and plant growth promotion systems under severe salt, drought, acidity, temperature, and heavy metal stresses is also highlighted.

7.2 Legume-*Rhizobium* Symbiosis Under Soil Acidity Constraints and Their Performance

Rhizobia-legume symbiosis is the most environment-friendly gadget that money owed for nearly 40% of all biologically fixed nitrogen estimated at 70 million lots per annum (Yadav and Verma 2014). Symbiotic nitrogen fixation is in need of host plant cultivar, *Rhizobium* strain and the interactions of these symbionts with the pedoclimatic elements and the environmental conditions. Extremes of soil acidity have an effect on nodulation by way of lowering the colonization of soil and the legume rhizosphere by means of rhizobia. Highly acidic soils ($pH < 4.0$) regularly have low ranges of phosphorus, calcium, and molybdenum and high concentrations of aluminum and manganese which are regularly poisonous for each partner. The terrible results of soil acidity on soil biodiversity and crop boom are associated to the deficiency of principal nutrients and toxicity of metals (Bordeleau and Prévost 1994; Chimdi 2015). Soil acidity influences soil productivity in the Ethiopian Highlands the place where faba bean cultivation is distinguished (Birhanu 2014). Most species of legume family can fix atmospheric nitrogen (N_2) by using symbiotic microorganism (rhizobia) in root nodules. Lateral gene transfer of particular symbiosis genes inside rhizobial genera is a vital mechanism permitting legumes to form symbiosis with rhizobia adapted to particular soils (Andrews and Andrews 2017). Symbiotic nitrogen fixation is an essential contributor to soil fertility. The nodulation process for almost all legumes studied is initiated by means of the legume production of a mix of compounds, mainly flavonoids, which persuade the synthesis of NodD protein in rhizobia leading to root nodule formation (Downie 2014).

Field competition experiments carried out in Southern Spain and one of a kind inoculant strains of *Sinorhizobium fredii* have been selected that can nodulate soybean in alkaline or acidic soils (Albareda et al. 2009). Novel strains of the β-proteobacteria *Burkholderia* are successfully nodulating herbaceous legume *Rhynchosia ferulifolia* with attainable position in nitrogen fixation adapted to acid, infertile soils (Garau et al. 2009). Nodulation and quantities of nitrogen fixed via legumes in acidic soils are reduced both through direct effects on the survival and multiplication of rhizobia and on the boom of the host flora (Giller 2001). The establishment of an effective symbiosis requires (a) colonization and survival in soil by way of rhizobia as saprophytes in competition with other endogenous microbes; (b) a fast colonization of the rhizosphere prior to root infection and genetic compatibility between host and root nodule bacteria to establish an effective nodule; and (c) a favorable environment to permit maximum fixation (Bordeleau and Prévost 1994). Therefore, the production of legumes in agriculture often requires the introduction of symbiotically potent root nodule bacteria as inoculants.

7.3 Phytobeneficial Traits of Rhizobia

PGPR greatly and rhizobia singly perform necessary function in improving plant growth through numerous mechanisms. The mode of action of these microbes to promote plant growth embraces (1) abiotic stress tolerance in plants; (2) nutrient fixation for easy uptake by using plant; (3) plant growth regulators; (4) production of siderophores; (5) production of unstable (volatile) organic compounds; and (6) production of protection enzyme like chitinase and ACC deaminase for the prevention of plant diseases as displayed in Fig. 7.1 (Choudhary et al. 2011; García-Fraile

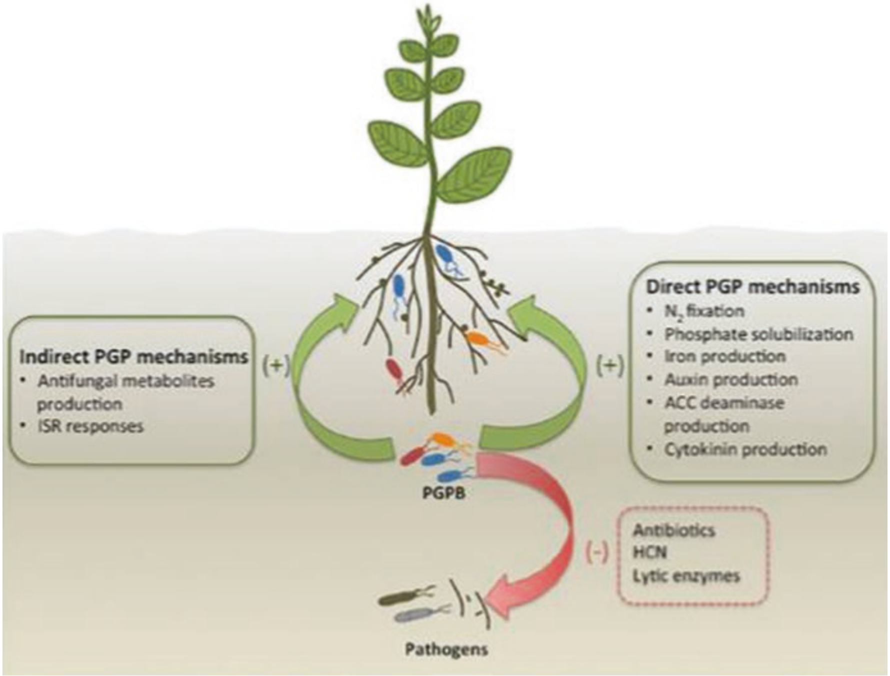

Fig. 7.1 The modes of action for PGPR are based on either direct and/or indirect mechanisms. (Adapted from Di Benedetto et al. 2017).

et al. 2015). However, the mode of action varies depending on the type of the host plants. Plant growth is influenced via a range of stresses due to the soil environment, which is a fundamental constraint for sustainable agricultural production. Beneficial interactions among plants and microbes are essential for stabilizing natural communities and restoring degraded lands for plant productivity (Premachandra et al. 2016). PGPR and rhizobia improve plant growth either directly, by facilitating resource use or modulating plant hormone levels, or indirectly by reducing the inhibitory outcomes of various pathogenic agents (Di Benedetto et al. 2017). The current knowledge of rhizosphere microorganisms in biotechnology and environment applications has been suggested by numerous scholars (Bakker et al. 2013; Glick 2012; Mendes et al. 2013). The main plant growth-promoting potentials (traits) of rhizobia are discussed below:

7.3.1 Siderophore Production

Iron is an integral nutrient for ideal plant development, and it is a cofactor in metabolic pathways. In contrary, its deficiency can also lead to disruption of respiration or photosynthesis (Rajkumar et al. 2010). Under stipulations of iron hindrance, various rhizosphere microbes produce siderophores, ferric iron-specific ligands, which may additionally beautify plant growth with the aid of increasing availability of iron close to the roots. Study done on chickpea (*Cicer arietinum* L.) with the application of *Rhizobium ciceri* has shown siderophore production for plant growth (Berraho et al. 1997). The utilization of rhizobia may also be one way to extend soil iron availability in the rhizosphere. Bacteria are capable to synthesize low molecular weight siderophores involved in the process of chelating ferric iron from the environment. As studies indicate, they have a strong ability to chelate ferric ions allowing their solubilization and extraction from most mineral or organic complexes (Sandy and Butler 2009). When iron is limited in the soil, iron-solubilizing microbes furnish vegetation with iron and better their growth. Experiment done on strawberries (Flores-Félix et al. 2015) confirmed siderophores producing *Phyllobacterium* strain resulted in its growth and quality. In the soil the quantity of bioavailable iron is very low due to its accumulation as iron oxides and hydroxides that cannot be simply utilized with the aid of residing organisms (Kraemer 2004). Thus, there is a competition for iron, wherein siderophore-producing PGPR facilitates plant iron acquisition from iron-limited environment, which helps to sequester iron from neighboring microorganisms outcompeting them (Yu et al. 2011; Ahmed and Holmström 2014). Likewise, plant pathogens send off low amounts of bioavailable iron behind (Fones and Preston 2013). Different strains of rhizobia have been suggested nowadays to produce siderophores. This ability also confers upon nodule bacteria a selective advantage and may additionally lead to both direct and indirect management of plant pathogens (Arora et al. 2001).

7.3.2 Plant Growth Regulators

Plant growth regulators (plant exogenous hormones) are artificial elements that are comparable to herbal plant hormones. They are used to adjust the growth of plant life and are necessary measures for boosting agricultural production. One of the terms for the prominent modes of action for growth promotion of rhizobial species is plant growth regulator. This is described as microorganisms that have the capability to produce or alter the concentration of growth regulators such as indole-3-acetic acid (IAA), gibberellic acid (GA), cytokinins (CK), and ethylene (Somers et al. 2004).

Auxin is one of the indispensable molecules, regulating most plant processes at once or in a roundabout way (Tanimoto 2005).The result found that auxin-producing *Bacillus* spp. inflicts a tremendous effect on *Solanum tuberosum*'s growth (Ahmed and Hasnain 2008). The most active and famous auxins in vegetation are IAA (Hayat et al. 2010). IAA impacts plant nutrition and improvement via altering cell division, extension, and differentiation with the aid of increasing the rate of xylene and root development (Glick 2012). According to Vacheron et al. (2013), a wide range of processes in plant developmental growth are controlled by exogenous IAA via stimulate primary root elongation in lower dose and primary root length, root hair, and formation of lateral roots in higher dose. IAA promote root hair elongation significantly and this help the plant to more nutrient uptake and promote their growth. Species of *Bradyrhizobium*, *Rhizobium*, and *Mesorhizobium* have been found to produce a considerable quantity of IAA under in vitro conditions (Ahmad et al. 2008). Studies have proven that inoculation of CK- or GA-producing PGPR stimulated plant growth (Xie et al. 1996; Joo et al. 2009). IAA producing PGPR increased plant growth in mung beans (Xie et al. 1996), rice (Bal et al. 2013), and *Brassica juncea* L. (Indian mustard) (Shim et al. 2015).

Ethylene is a hormone that serves many physiological tactics in plants. It acts at trace levels during the life of the plant by stimulating or regulating the ripening of fruit, the opening of flowers, and the abscission of leaves and synthesis of volatile organic compounds responsible for aroma formation in fruits to mention a few (Frankenberger Jr 2002; Glick 2014). The rhizobial species increase growth and induce physiological changes in plants via synthesis of enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase. Moreover, the higher dose of ethylene induces the defoliation and cellular processes that lead to the inhibition of root and stem growth and nitrogen fixation in legumes all of which in turn affect crop performance (Li et al. 2005; Ahmad et al. 2013). The plants synthesized ACC in response to exposure to more than a few types of environmental stress, such as cold, acidity, drought, pathogens, and heavy metals (Glick 2012). As a result rhizobia have the ability to degrade ACC in the rhizosphere and may want to shorten the deteriorating cycle and reconstruct a healthy root system that can withstand environmental stress. Ahmad et al. (2013) found that ACC deaminase-producing species of *Rhizobium* and *Pseudomonas* can improve the growth, physiology, and quality of mung beans under salt-affected environments. By lowering ACC levels in plants, rhizobia limit plant ethylene ranges which when exist in high concentrations can lead to a decreased plant growth and ultimately plant loss of life (Glick et al. 2007). The use of ACC deaminase-producing bacteria in association with different types of biotic and abiotic stresses results in enhanced plant tolerance to the stresses (Ma et al. 2003; Nascimento et al. 2012). ACC deaminase-producing rhizobial strains are 40% more environmentally friendly and effective at forming nitrogen-fixing nodules than non-producer (Ma et al. 2003). Generally, plants nodulated with the engineered strain of rhizobia resulted in a larger dry weight, a diminished ethylene level in roots, and a higher total copper uptake, in relation to indigenous strain.

7.3.3 Growth Modulation Enzyme

The synthesis of different antibiotics is often related with the potential of the bacteria to stop the proliferation of plant pathogens (generally fungi) (Mazurier et al. 2009). PGPR promote plant growth by producing different lytic enzymes together with chitinases, cellulases, glucanases, proteases, and lipases that can degrade part of the cell walls of many pathogenic fungi. Microorganisms that produce one or more of these lytic enzymes have been found to have biocontrol activity toward a range of pathogenic fungi inclusive of *Botrytis cinerea*, *Sclerotium rolfsii*, *Fusarium oxysporum*, *Phytophthora* spp., and *Rhizoctonia solani* (Kim et al. 2008; Glick 2012). The *Sinorhizobium fredii* KCC5 and *Pseudomonas fluorescens* LPK2 produce chitinase and beta-glucanases and dictate the fusarium wilt produced by *Fusarium udum* (Kumar et al. 2010). Apart from exhibiting the production of chitinase and beta-glucanases, *Pseudomonas* spp. inhibits *Rhizoctonia solani* and *Phytophthora capsici*, two of the most destructive crop pathogens in the world (Arora et al. 2008).

7.3.4 Nutrient Availability for Plant Uptake

Both free-living PGPR and symbiotic rhizobia have the potential to boost the availability of nutrient concentration in the rhizosphere by means of fixing nutrients, therefore stopping them from leaching (Choudhary et al. 2011). For instance, nitrogen is the most limiting nutrient for synthesis of amino acids and proteins in plants. It is a nitrogen present in the atmosphere (dinitrogen, N_2 or elemental nitrogen) and a relatively nonreactive molecules which is converted into ammonia through biological nitrogen fixation by most microorganisms (Lloret and Martínez-Romero 2005). The free-living PGPR *Azospirillum*, often related with cereals in temperate zones, is able to enhance rice crop yields (Tejera et al. 2005). Plants can't directly take up compounds like nitrogen, iron, and phosphate which are plentiful in the soil unless atmospheric nitrogen is converted via nitrogen fixation process (Chaparro et al. 2014; Richardson et al. 2009). Many researches have shown that *Rhizobium* spp. is the main nitrogen-fixing organism agriculturally known and regularly used to inoculate plants to increase nodules and plant biomass (Uribe et al. 2010). Some PGPR have phosphate solubilization capacity (Wani et al. 2007), insuring an increased phosphate ion availability and ease of uptake by plants. Agronomically vital rhizospheric actinobacteria *Kocuria turfanensis* strain 2M4 was discovered to be a phosphate solubilizer and IAA and siderophore producer (Goswami et al. 2014). Yadav et al. (2014) studied the positive effect of PGPR on nutrient uptake in rice via the inoculations of *Pseudomonas fluorescens* and *P. putida*. Phosphorus is also plant growth-limiting nutrient following nitrogen. Phosphorus is an essential nutrient required relatively in large amount and critical determinant of plant growth and productivity (Haileselassie et al. 2011). The requirement of phosphorus for faba bean is pretty high between 20 and 30 kg P ha^{-1} (Hungria et al. 2005). Moreover, it has precise roles in N_2 fixation, nodule initiation, nodule number, growth, and development (Schulze et al. 2006). It additionally performs an essential position in increasing legume yield through its impact on plant and fixation process by *Rhizobium* (Saraf and Dhandhukia 2005). On the other hand, phosphorus deficiency reduces N_2 fixation due to lowered nodule formation and decreased nodule sizes which ultimately affect the yield and grain quality and quantity (Sadeghipour and Abbasi 2012). Inoculation of high-quality *Rhizobium* had distinguished results on nodulation, growth, and yield parameters of faba bean (Desta et al. 2015).

7.4 Soil Acidity-Tolerant *Rhizobium* and the Symbionts for Sustainable Agriculture

Due to an extremely fast population growth and environmental pressure, it is mandatory to increase agricultural productivity with reduced environmental impacts. With the framework of sustainable agriculture, soil inoculation with PGPR and rhizobia is regarded as a promising bio-tool (Di Benedetto et al. 2017). The legume-*Rhizobium* symbiosis has tremendous ecological and agronomic importance with a full-size supply of nitrogen (Dita et al. 2006). Globally, N_2 fixed by using nodulated legumes makes contributions of 21.45 Tg nitrogen yearly in the world (Herridge et al. 2008). Among legumes, faba bean contributes to sustainable agriculture via fixing atmospheric nitrogen symbiotically with rhizobia. Effective symbiotic nitrogen fixation of faba bean with fast-growing species of *Rhizobium leguminosarum* bv. *viciae* is well known. Later, *R. fabae*, *R. laguerrereae*, *R. etli*, and *Agrobacterium tumefaciens* had been also recognized as faba bean-nodulating micro-symbionts (Tian et al. 2008; Youseif et al. 2014).

The application of *Rhizobium* in faba bean performs major functions in soil acidity enhancement. These bacteria can facilitate the overall growth of legumes and related nonlegumes directly by means of transferring symbiotically formed N to crops like cereals, growing in intercrops (Hayat et al. 2008). Besides N_2 fixation, rhizobia promote the growth of plant life via means of different mechanisms together with production of plant growth-promoting substances like phytohormones; auxins, cytokinins, and abscisic acids; and vitamins (Ahmad et al. 2008; Wani et al. 2007). Declining in soil fertility, acidity, decreased N_2 fixation, over cultivation, and poor soil management resulted in lower yields in leguminous crops (Abubakari et al. 2016). The different stages of plant host and rhizobial interaction in the interaction have been affected by acidity via limiting production of nodulation factors, attachment of rhizobia to roots, number of root nodules, and the nitrogenase activity (Graham 1992; Morón et al. 2005). To keep away from acidic soil losses in leguminous crop productivity, the improvement and viable strategies in legume-rhizobia associations or the selection of rhizobia capable to tolerate acidity has been designed (Ruiz-Díez et al. 2009). The key in acidity tolerance is the improvement of acid-tolerant and effective rhizobia inoculants (Tittabutr et al. 2006). Many experimental results have shown that it is feasible to enhance the growth of leguminous trees with superb rhizobia inoculation (Bogino et al. 2006; Maia and Scotti 2010).

Soil pH is one of the most limiting factors in legume and *Rhizobium* symbiosis as it renders rhizobial survival, nodulation, and N_2 fixation. McDonald (2014) noted that rhizobia are extremely sensitive to acidic pH and soluble aluminum ions between soil pH 4.8 and 5.0 as pH much less than 4.6 inhibits their activity. Legumes and *Rhizobium* form efficient symbiosis and fix high quantity of nitrogen when soil pH is no less than 5.6–6.1. On contrary, nitrogen fixation can be decreased up to 30% below $pH<4$. Findings of Ambrazaitienė (2003) and Hartwig and Soussana (2001) have been showed that soil acidity inhibited the root hair infection and nodulation; this disrupts the communication process. Furthermore, experimental outcomes have been revealed that soil acidity hinders the distribution and symbiotic efficiency of *R. leguminosarum* bv. *trifolii*, *R. leguminosarum* bv. *viciae*, *Sinorhizobium meliloti*, and *R. galegae*. In a slightly acidic soil, the average number of rhizobia has been 540.0×10^3cfu $g^{-1}$of soil, whereas, in high and medium acidic soil (pH KCl 4.1–5.0), *R.galegae* and *Synorhizobium meliloti* are no longer available. The symbiotic effectiveness is strain-specific where some that are outcompeted under normal pH conditions ($pH > 5.5$) might become dominant under low pH ($pH < 5.5$) conditions (Ferguson et al. 2013). *Bradyrhizobium* sp. are generally more acid-tolerant than most *Rhizobium* sp. (Brockwell et al. 1991). Although few rhizobia thrive at $pH < 5$, certain strains of *R. tropici* and *R. loti* are highly acid-tolerant (Appunu and Dhar 2006).

7.5 Role of *Rhizobium* Inoculation in Organic Farming Systems

Soil is a crucial and biologically active resource in agricultural ecosystem. It is to mean industrial agriculture that involves the application of agrochemicals (synthetic fertilizer, pecticides, herbicides and other fabricated inputs) (Pelletier et al. 2008). The experimental outcomes of Muleta (2007) have validated that the rational exploitation of microbial inputs in Ethiopian *Coffea arabica* production systems deserves inoculum development while retaining environmental quality. Due to these advantages, organic agriculture reached 43.1 million hectares by the end of 2013, with a yearly escalation of 14% (Syswerda et al. 2012; Cavigelli et al. 2013). Biological nitrogen fixation (BNF) is becoming economically feasible and eco-friendly eye-catching agricultural input (Bekere et al. 2012). As a result, legume plants symbiotically fix about 33 to 46 teragram (Tg) of nitrogen per year in the world (Herridge et al. 2008). Faba bean alone can fix nearly 150–300 kg N ha^{-1} in a growing season (Singh et al. 2012). BNF can be more desirable by means of effective and persistent *Rhizobium* seed inoculation. In this regard, pulse crop *Rhizobium* inoculation can fix better nitrogen to eliminate the need for nitrogen fertilizer inputs (Walley et al. 2007). Numerous studies proved that in improved yields with inoculation, Haile et al. (2008) reported a yield gain of 61–68% and 52% in *R. leguminosarum* var. *viciae*-inoculated faba bean in Bulie and Chencha districts of Southern Ethiopia, respectively. In Iran similar result has been mentioned that inoculation of faba bean seed with an appropriate strain increased faba bean grain yield by 35–69% (Khosravi et al. 2001). Abdel-Aziz and El-Din (2015) of Egypt described yield increments between 5.6–20% in Kantara and 6.5–15.4% in Gelbana at North Sinai via *Rhizobium* inoculation as compared to uninoculated treatment (control). The bacterial genera of *Pseudomonas*, *Klebsiella*, *Enterobacter*, *Azospirillum*, *Bacillus*, *Rhizobium*, *Alcaligenes*, and *Arthrobacter* have been said to enhance plant growth directly or indirectly (Saharan and Nehra 2011). In Australia competent and reliably faba bean rhizobial inoculant strains have been observed that can form nodules in soils above pH 5.0; however they are restricted below this level. The performance of strains of rhizobia with improved acidity tolerance to improve pulse nodulation and N_2 fixation on acidic soils has been also suggested (Denton et al. 2018).

7.6 Molecular Basis of *Rhizobium*-Mediated Mitigation of Soil Acidity Stresses

Environmental stress such as soil acidity, salinity, drought, and temperature imposes a foremost threat to each symbiotic nitrogen fixation and agriculture. For this reason, the *Rhizobium*'s tolerance to one of a kind environmental stresses is a preferred property for use in nitrogen-depleted soils (Lebrazi and Benbrahim 2014). Many research outcomes have mentioned unfavorable consequences of the aforementioned constraints on the survival and proliferation of rhizobia (Elboutahiri et al. 2010). Of these, soil acidity adversely impacts the survival, multiplication, and development of symbiosis of rhizobia and can affect each symbiosis partners. Nearly neutral or slightly acidic soil has been preferred for the growth of nitrogen-dependent leguminous plants (Zahran 1999). The most appropriate pH for rhizobial growth is considered to be 6.0 and 7.0. Acidic soil can have an effect on the production and excretion of nodulation factors of *R. leguminosarum* bv. *trifolii* (Kantar et al. 2010). The rhizobial strains vary extensively in their acidity tolerance. Although some previously proven acid-tolerant rhizobia strains have been chosen (Laranjo and Oliveira 2011), the mechanisms that appoint life on and growth in acidic soils have not been fully explained; consequently the molecular basis for variations in pH tolerance among strains of rhizobia is still no longer clear. In the last decades, the most important strategies employed to reduce the negative results of unfavorable environment on legume production have been centered on the selection of host genotypes adapted to drastic conditions (Bargaz et al. 2013; Farissi et al. 2011). Nevertheless, the exploration on rhizobial strains may represent any other approach to enhance plant productiveness via symbiosis or adaptation to a number of environmental hindrance (Keneni et al. 2010).

7.6.1 Molecular Basis of Soil Acidity Tolerance

The find out the molecular basis of stress response in rhizobia is fascinating considering that they are exposed to the soil conditions (da-Silva et al. 2017). The physiological and biochemical mechanisms of rhizobial adaptation to acidity conditions includes (1) exclusion and expulsion or extrusion of protons H^+ (Lebrazi and Benbrahim 2014); (2) increasing potassium and glutamate contents in the cytoplasm of stressed cells (Aarons and Graham 1991); (3) the change in the lipopolysaccharides composition (Vriezen et al. 2007); (4) the accumulation of polyamines (Fujihara and Yoneyama 1993); (5) the production of acid shock proteins (ASPs) (Foster 1993); and (6) the involvement of myriad genes such as *actA*, *act P*, *actR*, *actS*, *exoR*, *lpiA*, and *phrR* (Abd-Alla et al. 2014). All these mechanisms are valuable in rhizobial growth in acidic soil. These genes are proven to be crucial for rhizobia survival at lower pH soils (de Lucena et al. 2010). The work done by Kurchak et al. (2001) has identified 20 genes in *R. leguminosarum* that are responsible for acid stress, namely, *act* genes (acid tolerance).

The contribution of passive cytoplasmic buffering in maintaining active pH homeostasis has been mentioned. The main classes of active pH homeostasis mechanisms comprise coupling transmembrane proton movements to an energetically favorable exchange with cations (K^+, Na^+) or anions (Cl^-), a strategy that is the central active component of alkaline pH homeostasis (Padan et al. 2005; Krulwich et al. 2007), and metabolic switching to generate acidic or neutral end products (Stancik et al. 2002; Wei et al. 2006). Moreover, myriad outcomes has been recommended to retain optimal pH like acid-induced amino acid decarboxylases and base-induced amino acid deaminases (Foster 2004; Richard and Foster 2004); use of urease activity, sometimes working together with carbonic anhydrase activity, to regulate cytoplasmic and periplasmic pH (Stingl et al. 2002; Sachs et al. 2006; Sachs et al. 2005); and synthesis of acid-resistant membrane structures such as cyclopropane fatty acids (CFAs) (Cronan 2002) and tetra ether lipids (Baker-Austin and Dopson 2007) or increased synthesis of anionic phospholipids or specific neutral lipids at high pH and chaperone protection from temporary damage due to pH shift (Stancik et al. 2002). There is scant information on the physiological and genetic bases of acid tolerance in rhizobia. It has been shown that acid-tolerant strains of *R. meliloti* can more readily generate a pH gradient when grown in acidic soils to maintain a more conveniently internal pH as compared to acid-sensitive strains that failed to maintain it (O'Hara and Glenn 1994).

One approach microorganisms might also counteract changes in internal pH is via the buffering ability of cytoplasm with molecules including proteins, polyamines, polyphosphates, and inorganic phosphate. This buffering has been gained by protein amino acid side chains that can work over a wide range of pH. Both polyphosphates and inorganic phosphate have pKa values around 7.2 and thus may want to offer appropriate buffering ability near the most beneficial internal pH of neutrophils. As many studies suggested, polyphosphates have been involved in many extreme stress adaptations along with acid exposure of *Burkholderia* (Moriarty et al. 2006; Seufferheld et al. 2008). Polyamines are additionally related with acid resistance in bacteria (Wortham et al. 2007). Both polyphosphates and polyamines make a contribution to biofilm formation in which passive buffering would possibly furnish specific protection from pH shift.

Polyamines are low molecular weight natural compounds that exist in bacteria, animals, and plants consisting of putrescine (Put), spermidine (Spd), and spermine (Spm) (Hussain et al. 2011). These molecules are widely implicated in cell division and differentiation, root elongation, fruit ripening, leaf senescence, DNA synthesis, gene transcription, protein translation, and chromatin organization (Alcázar et al. 2011; Zhang et al. 2011; Alet et al. 2012; Tavladoraki et al. 2012). Polyamines additionally play vital roles in salt-, acid-, drought-, temperature-, ozone-, flood-, heavy metal-, and oxidative stressed environments (Cheng et al. 2009; Tavladoraki et al. 2012). Multiple abiotic stresses can modulate polyamine biosynthetic, metabolic pathway and its levels. Polyamines share common substrates with nitric oxide (NO), ethylene, and proline as well as N metabolism, so finding the link between polyamines and abiotic stress is complicated (Shi et al. 2013).

Root nodule microorganisms have employed a crucial mechanism of retaining intracellular pH. They exhibit acidity tolerance (adaptation) response by protecting against an extreme acid shock. Variations in acid tolerance within species of root nodule bacteria suggest a genetic basis to low pH tolerance, and studies of acid-sensitive mutants suggest that as many as 20 genes could be involved (Glenn and Dilworth 1994). Experimental results have found that there are a sensor and a regulator (actR and actS) genes in *S. meliloti* that encode for acid shock response (Tiwari et al. 1996a). The membrane-bound product of actA is basic and responsible for maintaining internal pH at around 7, when the external pH drops below 6.5 (Tiwari et al. 1996b). They demonstrated that mutants defective in this gene are unable to maintain intracellular pH and cannot grow at a pH lower than 6. Tiwari et al. (1996b) indicated that calcium is involved in acid tolerance mechanism of *S. meliloti*. Riccillo et al. (2000) reported that glutathione plays a key role in acid tolerance of *Rhizobium tropici*. Glutathione also provides protection against chlorine compounds in *Rhizobium leguminosarum* bv. *phaseoli* (Crockford et al. 1995). The activation of glutathione synthesis might be essential for tolerance to acid stress (Muglia et al. 2007). TypA acts as a regulator by controlling the phosphorylation of proteins and is required for growth at acidic condition (Kiss et al. 2004). Reeve et al. (1998) show that, in addition to the genes like actA, actS, and actR that are absolutely essential for growth of *S. meliloti* at low pH, there is phrR gene which, while not essential for growth, appears to be induced by exposure to low pH. Munns (2005) found that *Rhizobium* which produces greater amounts of exopolysaccharides is able to survive in acidic conditions more successfully than *Rhizobium* that can only produce smaller amounts.

Adaptation of microorganisms to stress is a complex multilevel regulatory process in which many genes may be involved (Srivastava et al. 2008). Microbial intrinsic metabolic and genetic capabilities make them suitable organisms to combat extreme conditions of the environment (Singh 2014). Their interactions with the plants evoke various kinds of local and systemic responses that improve metabolic capability of the plants to fight against abiotic stresses (Nguyen et al. 2016). A testament to the important attributes of the microbial interactions with plants is significant number of accumulating pieces of evidence that suggest in-depth mechanisms based on plant-microbe interactions that offer modulation of cellular, biochemical, and molecular mechanisms connected with stress tolerance (Bakker et al. 2012). Microbial interactions with crop plants are key to the adaptation and survival of both the partners in any abiotic environment. Induced systemic tolerance (IST) is the term being used for microbe-mediated induction of abiotic stress responses. The role of microorganisms to alleviate abiotic stresses in plants has been the area of great concern in the past few decades (Nadeem et al. 2014; Souza et al. 2015). The role of several rhizospheric occupants belonging to the genera *Pseudomonas* (Ali et al. 2009; Sorty et al. 2016), *Azotobacter* (Sahoo et al. 2014), *Azospirillum* (Omar et al. 2009), *Rhizobium* (Remans et al. 2008; Sorty et al. 2016), *Bacillus* (Vardharajula et al. 2011), and *Bradyrhizobium* (Tittabutr et al. 2006) in plant growth promotion and mitigation of multiple kinds of abiotic stresses has been documented. The selection, screening, and application of stress (acid)-tolerant microorganisms particularly rhizobia, therefore, could be viable options to help overcome productivity limitations of crop plants in stress-prone areas.

Nitrogen-fixing symbiotic bacteria known as rhizobia can exist in different soils and adapt to different environmental conditions (Janczarek et al. 2010). Rhizobia infect the roots of legumes and induce the formation of nodules where the rhizobia fix nitrogen. Some typical environmental stresses faced by both partners of symbiosis include salinity, drought, temperature, soil pH, heavy metals, and so on (Küçük and Kivanc 2008). Therefore, limiting factors impose restriction and may affect symbiosis and productivity (Keneni et al. 2010). *Rhizobium* species appear to be varying in their symbiotic efficiency under acidic or alkaline conditions (Ali et al. 2009). Extreme pH affects nodulation by reducing infection by rhizobia. Highly acidic soils and highly alkaline soils (pH 8.0) affect survival, the growth of both partners, and reduce nitrogen fixation (Bordeleau and Prévost 1994). The capacity of *Rhizobium* spp. to adapt to adverse soil acidic condition is fundamental for the establishment of an efficient symbiosis. More than one-quarter of the world's cultivable soils are acidic, which makes the study of the mechanisms implied in the survival to acid stress of great agricultural relevance (Tiwari et al. 1996a).

7.6.2 Survival and Persistence of Rhizobia in Acidic Soils

Soil acidity impacts on the number of population and survival of rhizobia in the soil. As a result, the number of rhizobia is generally less than 100 per g of soil below 5.5 pH ($CaCl_2$), the threshold below which there is a proper possibility of the response to inoculation (Drew et al. 2012). Similarly, Drew et al. (Drew et al. 2012) has indicated that rhizobia population are much less than 10 per g of soil below pH 4.5 in the fields of field pea. The growth, survival, abundance, and competitiveness in nodulation ability of rhizobia are incredibly influenced by soil pH (Brockwell et al. 1991). However, bacteria and archaea have the potential to maintain pH homeostasis usually closer to neutrality via cytoplasmic buffering (Slonczewski et al. 2009). Experimental finding stated that nearly 10^{-3} decreased the number of *S. meliloti* in soils with pH< 6 as compared to pH >7.0 (Brockwell et al. 1991). Although few rhizobia thrive at pH < 5, certain strains of *R. tropici* and *R. loti* are highly acid-tolerant (Graham et al. 1994). Some species of rhizobia are pretty tolerant to acidity. *B. japonicum* can continue to exist in acidic soils down to a pH of 4.0, whereas *R. leguminosarum* bv. *trifolii* and bv. *viciae* can't grow under pH 4.7; the lower limit for most *S. meliloti* strains is pH 5.0 (Hirsch 1996). The following different intracellular pH maintenance techniques have been appointed by rhizobia: (1) decreased membrane permeability; (2) internal buffering; (3) amelioration of external pH; (4) proton extrusion/uptake; and (5) prevention of metal ion toxicity. Changes in soil pH are regarded to be related with shifts in the dominant rhizobial groups within soil populations (Fig. 7.2). The result finds that, below a pH of 4.2, *Rhizobium* spp. of *R. etli*, *R. giardinii*, and *R. gallicum* groups has dominated the populations, while the

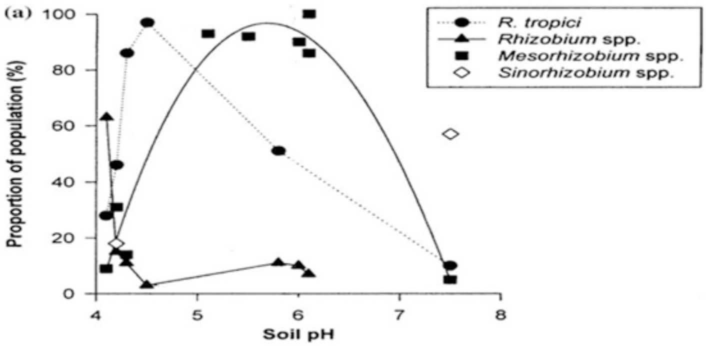

Fig. 7.2 Relationships between the relative dominance of rhizobial types and soil pH. (Adapted from Bala and Giller 2006)

R. tropici groups have been dominant between pH of 4.2 and 5.0. The *Mesorhizobium* spp. had been the most dominant between pH 5.0 and 6.5, whereas the *Sinorhizobium* spp. conquered above a pH of 6.5 (Bala and Giller 2006). Similar outcome has been forwarded in low pH (acidity) adaptation and dominancy of *R. tropici* (Graham et al. 1994). The rhizobial population in general has proved to greater survival capacity in acidic soils than in YEM broth at same low pH level. The reasons of tolerance and higher survival in rhizobia may be due to the attachment of rhizobia with cations/anions or organic molecules in the soil than in YEM broth (Appunu and Dhar 2006). Therefore, the establishment of a relationship between rhizobial types and soil conditions, mainly soil acidity, may want to have an extensive effect on the survival and persistence as well as to predict the adaptability of inoculant strains to specific soil types and conditions.

7.6.3 Rhizobium-Legume Molecular Signaling Exchange

The interaction of legume-*Rhizobium* symbiosis is initiated via a complex signaling dialogue between each partner to permit the entry of rhizobia into the root and the development of nodules for atmospheric nitrogen fixation to be available to and assimilated by plants. There has been a mutual symbiosis between rhizobia and legumes for the exchange of signal molecules among them (Downie 2014; Nelson and Sadowsky 2015). The signal molecules produced by each partner have been involved in early steps of symbiosis and have been identified through the evaluation of molecular mechanisms of plant-rhizobia communication primarily based on signal exchange (Tseng et al. 2009). Nodulation and symbiotic N_2 fixation contain many rhizobial genes commonly designated as symbiosis genes, such as *nod* and *nif* genes (Cooper 2007). As analyzed by the same author, the genes nod ABC (transcriptionally regulated by using NodD) encode enzymes that synthesize Nod elements (lipo-chito oligosaccharides). This gene has been perceived by using the plant, activating the root hair curling, and forming a hook for subsequent improvement of an infection thread (Cooper 2007). Nevertheless, preceding research has proven that chaperone proteins, such as GroEL and ClpB, typically involved in stress response, may also play essential roles in the symbiotic legume-rhizobia relationships (Brígido et al. 2012).

7.7 The Position of *Rhizobium* in Other Plant Stress Tolerance

Abiotic stresses are considered to be the most important sources that can be restricted in agricultural yield reduction. However, the depth of these stresses varies depending on the type of soils and plant factors (Nadeem et al. 2010). Due to their sessile nature, plants have continuously been confronted with myriad number of abiotic and biotic stresses in their immediate environment. All plants have been perceived and respond to one of the following stress signals of drought, soil acidity, heat, salinity, herbivory, and pathogens (Hirt 2009). PGPR can enhance plant growth under abiotic stresses and may consequently open new applications for sustainable agriculture (Egamberdieva and Kucharova 2009). A research suggests that the following bacterial genera *Rhizobium*, *Bacillus*, *Pseudomonas*, *Paenibacillus*, *Burkholderia*, *Achromobacter*, *Azospirillum*, and many others have been stated to provide tolerance to host plants under different abiotic stress environments (Grover et al. 2011).

7.7.1 Temperature

Temperature is one of the principal elements affecting rhizobial growth and survival and the symbiotic process (Niste et al. 2013). When soil temperature is either too high or too low, it can limit legume BNF, nodulation, and nodule establishment and nitrogenase activity although it varies among species. The optimal soil temperature for fixation has to vary between 25 and 30 °C. However, a consistently cool-temperature region around the root can significantly prolong the onset of nitrogen fixation in contrast to optimal temperature (Abendroth et al. 2006). Resistance/tolerance to excessive temperature is thus an acceptable property for rhizobial inoculants to be used. Various researches have been carried out to examine the growth responses of different *Rhizobium* strains to increasing temperatures.

7.7.2 Drought Stress

Drought stress is an increasing hassle that can limit crop production in the world under current climate change scenarios. As a result a great and renewed attention is paid for rhizosphere microorganisms that have been ameliorating plant stress with the aid of various mechanisms that span plant hormone level modification and bacterial exopolysaccharide production (Kaushal and Wani 2016; Naveed et al. 2014).

From experimental findings, drought predominantly decreased world food production by 9–10% (Lesk et al. 2016). As studies suggest, plants can adapt (cope) to this devastating impact via morphological adaptations, osmotic adjustment, optimization of water resources, antioxidant systems of reactive oxygen species (ROS) linked to drought, and induction of a variety of stress-responsive genes and proteins (Farooq et al. 2009). To date, introduction of drought-tolerant cultivars has been the strategy used to mitigate the negative effects of this stress on crops and their yields (Eisenstein 2013). The aforementioned techniques overlook the ecological context of the soil environment in which the crops are grown. Therefore, there is a necessity for microbial-based tactics to mitigate drought stress. This is why rhizosphere microbial communities have received firsthand attention for enhancing crop productivity and stress resistance (Glick et al. 2007; Yang et al. 2009). Numerous studies forwarded the best studied plant-associated microbes comprising mycorrhizal fungi (Azcón et al. 2013), nitrogen-fixing bacteria (Lugtenberg et al. 2013), and plant growth-promoting rhizobacteria (Glick 2012). The beneficial roles of these microbes have been observed in nodulation, growth promotion, and biocontrol enhancement in plant growth under drought stress conditions. The capability of microorganisms such as rhizobia to live on drought stress environments depends on their competency to cope with radiation stresses, reactive oxygen species (ROS), solutes, and temperature extremes (Deaker et al. 2004). The progressive result of PGPR and rhizobia on plants under abiotic stresses is the improvement of leaf water status, especially under salinity and drought stress (Ahmad et al. 2013).The finding of Sarma and Saikia (2014) stated that *Pseudomonas aeruginosa* strain inoculation has improved the growth of *Vigna radiata* (mung beans) plants under drought conditions. Similarly, Ahmad et al. (2013) and Naveed et al. (2014) found that the stomatal conductance (water vapor exiting through the stomata leaf) of plant leaf has been greater in PGPR-inoculated plants than the noninoculated in drought situations. The discovering result from each research proves that PGPR-inoculated plants have a tendency to enhance the water-use efficiency of plants. This finding ought to be beneficial in terms of decreasing immoderate utilization of water (Mnasri et al. 2007). Similar result conducted in vitro by Swaine et al. (2007) reported that strain of *Bradyrhizobium elkanii* isolated from a drought environment has been more tolerant to osmotic stress than strains isolated from wet environments. *Achromobacter piechaudii* ARV8 which produced ACC deaminase conferred IST against drought and salt in pepper and tomato (Mayak et al. 2004). Moreover, Grover et al. (2014) has mentioned that sorghum plants treated with *Bacillus* spp. strain KB 129 under drought stress showed 24% increase in RWC over plants that have been no longer treated with PGPR. Similar consequences have been validated in maize crop (Naveed et al. 2014).

7.7.3 Salt Tolerance

Soils affected via salt harasses are known to destroy the growth of plants (Paul 2013). The true indications of the problem have been stated as nearly 40% of the world's land surface is affected by means of salinity-related issues (Zahran 1999). Enhanced salt tolerance in maize upon co-inoculation with *Rhizobium* and *Pseudomonas* is correlated with reduced electrolyte leakage and retention of leaf water contents (Bano and Fatima 2009). Similarly results from Marulanda et al. (2010) suggested that *Bacillus megaterium* strain inoculated into maize roots elevated the potential of the root to take in water under the salinity conditions. Gond et al. (2015) also found comparable behavior when *Pantoea agglomerans* is used to be inoculated into the maize roots. All these results forwarded that the capacity of the maize root to absorb water in saline conditions has improved. Here, microorganisms that can grow under hypersaline environments have better capability to colonize rhizospheres and external spaces of roots that are themselves exposed to high salinity conditions. Thus, the strategy was to first screen the bacterial isolates for their ability to grow under hypersaline conditions. More likely, Gonzalez et al. (2015) used *Azospirillum brasilense* in in vitro studies to enhance salt tolerance in jojoba plant. This finding forwards that *A. brasilense* can limit the undesirable effects of salinity on the jojoba rooting. This suggests that *A. brasilense* has greater plant tolerance to salt stress. Generally, the potential roles of co-inoculated *Rhizobium* and *Pseudomonas* in salt tolerance of *Zea mays* have been due to increased production of proline along with diminished electrolyte leakage, maintenance of relative water content of leaves, and selective uptake of K ions (Bano and Fatima 2009). Other experimental investigation found that inoculation of lettuce with *Azospirillum* sp. under salt-affected soil improves lettuce quality, extends the storage life, and increases yield (Fasciglione et al. 2015). Moreover, Yao et al. (2010) reported that inoculation of *P. putida* Rs198 promoted cotton growth and germination under conditions of salt stress.

7.7.4 Heavy Metals (HMs) Stress

In the era of civilization, HMs pollution has numerous environmental, human health, and agricultural problems. As different results indicated, the uptake of HMs from soil has both direct and indirect effect on microbial composition (Rathnayake et al. 2013), metabolism (Dostal et al. 2012), and differentiation (Harrison et al. 2007). The metal species, habitat of interacting organisms, structure and compositions, and microbial functions have been disturbing the interaction of metals with soil microbes. Heavy metals at minimal dose are required for more than a few metabolic activities of microbes along with rhizobia and legume crops. To the contrary, the elevated doses of HMs cause undeniable damage to rhizobia, legumes, and their symbiosis (Ahmad et al. 2012). Different findings presented the toxic effect of greater quantities of metals on physiological processes like synthesis of chlorophyll pigments of plants (Feng et al. 2010) and (Ahmad et al. 2008) inactivated protein synthesis. Similar result suggests that the destructive impact of sludge application on N_2 fixation in faba bean is pronounced as this amendment comprises toxic HMs (Chaudri et al. 2000). Certain metals like Cu, Zn, Co, and Fe are essential for survival and growth of microbes. However, these metals can have toxicity impact at greater concentrations and may inactivate protein molecules (Samanovic et al. 2012). Thus, microorganisms have advanced some mechanisms to overcome the inhibitory results of toxic HMs. Some of the HM cleaning techniques adopted via microbial communities are (i) metal exclusion using permeable barriers; (ii) active transport of HMs far from the cell; (iii) intracellular sequestration through protein binding; (iv) extracellular sequestration; (v) enzymatic cleansing of HMs to a less toxic form; and (vi) decreasing the sensitivity of cellular targets to metal ions. As results indicated, both single and multiple detoxification mechanisms have been affected by microbial types involved (Shoeb et al. 2012).

Rhizosphere microbes perform an extensive function in phytoremediation of HM-contaminated soil and have the mobility and availability to the plant by means of chelating agents, acidification, phosphate solubilization, and redox changes (He and Yang 2007). In order to live on HM-contaminated soils, tolerance has to be present in microbes and the host plants. Experimental results supported that application of nitrogen fixing rhizobia and PGPR in heavy metal contaminated soil resulted in significant reduction in the level of HMs in the soil. These soundful outcomes have been observed in the overall improvement in the growth and yield of chickpea and pea (Gupta et al. 2004; Wani et al. 2007). A similar finding recently suggested that *Methylobacterium oryzae* CMBM20 and *Burkholderia* sp. CMBM40 strain inoculation in nickel- and cadmium-treated soil appreciably decreased their toxicity effect in tomato via promoting growth in greenhouse test (Madhaiyan et al. 2007). Additionally, application of *Pseudomonas maltophilia* strain transformed the mobile and toxic form of chromium (Cr VI) to nontoxic and immobile form (Cr III) and also minimized the mobility of other toxic ions, such as Hg^{2+}, Pb^{2+}, and Cd^{2+} (Khan et al. 2009).

7.7.5 Induction of Plant Resistance

In the last few decades, the world has seen an increased application of un-ecofriendly synthetic fertilizers in agriculture. This situation shifts in the use of PGPR strains that can trigger the resistance in plants against pathogens. This phenomenon is referred as induced systemic resistance (ISR). Plants have the capacity to acquire a state of ISR to pathogens after inoculation with PGPRs (Pieterse et al. 2003). In plant roots, PGPRs can lead the plant innate immune system and confer resistance to a broad spectrum of pathogens with a minimal impact on yield and growth (van Hulten et al. 2006). Phytopathogenic microbes have massive effect in agriculture and considerably decreasing crop yields and causing total crop loss (Antoun and Prévost 2005). As different studies forwarded, root-colonizing species of *P. fluorescens*, *P. putida*, *B. pumilus*, *Serratia marcescens*, *Paenibacillus alvei*, *Acinetobacter lwoffii*, *Chryseobacterium balustinum*, and *Azospirillum brasilense* protect large variety of plant species against foliar diseases in greenhouse and field trials (Pieterse et al. 2003; van Loon 2007). In the same fashion, various rhizobial species of *R. etli*, *R. leguminosarum* bv. *phaseoli*, and *R. leguminosarum* bv. *trifolii* have been pronounced to induce systemic resistance in plants with the aid of producing bio-stimulatory agents (Gohel et al. 2006; Mishra et al. 2006). A number of phytobeneficial microbes of *P. fluorescens* (Peighami-Ashnaei et al. 2009) and *B. subtilis* (Dawar et al. 2010) have proven antagonism effect against *Fusarium* sp., *Pythium* sp., *Rhizoctonia* sp., *Sclerotium* sp., and diseases leading to enhancement in plant growth or yield. Moreover, application of *B. subtilis*, *Pochonia chlamydosporia*, and *P. fluorescens* can successfully manage the diseases brought on through nematode infection (Trabelsi and Mhamdi 2013). The excessive cost of pesticides, the emergence of fungicide-resistant pathogens, and different health-related influences of modern agriculture on the environment have increased interest in agricultural sustainability and biodiversity conservation by using phytobeneficial soil microorganisms (Van der Vossen 2005).

7.8 Co-inoculation of Rhizobia and Other Rhizobacteria

The inconsistency of results in single microbial inoculation under field application has brought an emphasis on co-inoculation (Bashan and De-Bashan 2005). Co-inoculation of rhizobia with PGPR plays an important role in promotion of nodulation and plant growth of leguminous plants. The statement is supported via co-inoculation of soybean with *Azospirillum* spp., and *Bacillus* sp. significantly increased 23.65 and 34.92% seed yield over single inoculation (Aung et al. 2013).

These outstanding findings push researchers focusing on co-inoculation of rhizobacteria and R*hizobium* to enhance the growth of legumes. PGPR provides a supportive role for *Rhizobium* inoculation in legumes by means of antibiotic, siderophore, and enzyme production to facilitate the infection sites for *Rhizobium* by colonizing the root surface (Contesto et al. 2008). The increase in the number of pods per plant of faba bean with co-inoculated *Rhizobium* strains and *P. fluorescens* is compared to the uninoculated (Radwan et al. 2005). Other finding also forwarded that co-inoculation of common bean with *Rhizobium* and PGPR sustainably increased shoot and root dry weights in respect to *Rhizobium* inoculation alone and the uninoculated control. Similarly, Figueiredo et al. (2008) reported a greater increase in shoot and root dry weight when CIAT 899 rhizobia strains and *Paenibacillus polymyxa* strain DSM 36 were inoculated together in common bean than single inoculation. Additionally, Elkoca et al. (2010) informed an elevated shoot dry weight as a result of co-inoculation of common bean with *Bacillus megaterium* (M-3) and *Rhizobium* strain. Once more, co-inoculation of P-solubilizing bacteria and *Rhizobium* stimulated plant growth over single inoculations (Charana Walpola and Yoon 2013). Experimental results of Tariq et al. (2012) indicated that non-rhizobial PGPR improved nodulation and grain yield of the legumes upon co-inoculation with crop-specific rhizobia. These improvement in growth and yield has been upon *Rhizobium* and *Pseudomonas* co-inoculation is related proline production, decreased electrolyte leakage, maintenance of relative water content and selective uptake of potassium ions in salt affected *Zea mays* (Bano and Fatima 2009). Furthermore, co-inoculation of PGPR and rhizobia has a synergistic effect on bean growth as PGPR allows *Rhizobium* with biofertilizers for common bean production

(Korir et al. 2017). Bai et al. (2003) also stated that co-inoculation of *Bacillus* strains in soybean plants with *Bradyrhizobium japonicum* provided the largest increases in nodule number, nodule weight, shoot weight, root weight, total biomass, total nitrogen, and grain yield.

Field study conducted in salt-affected soils has shown that single and combined inoculation of *Rhizobium* and PGPR enhanced growth, nodulation, and yield of mung bean in 1000 grain weight and grain yield up to 14 and 30%, respectively (Aamir et al. 2013). A comparable result has stated that dual inoculation of *P. pseudoalcaligenes* and *B. pumilus* protects paddy plant from abiotic stresses via induction of osmo-protectant and antioxidant proteins (Jha et al. 2011). Co-inoculation of *Bradyrhizobium* sp., *Paenibacillus polymyxa*, and *Bacillus* sp. brings increased nodulation and root dry matter in *Vigna unguiculata* (da Silva et al. 2007). Similarly, endophytic PGPR and nitrogen-fixing *Rhizobium* species have been found a synergism in N-fixation efficiency of lentils (Saini and Khanna 2012). Also, Wang et al. (2012) described that application of cucumber plants with a mixture of *Bacillus cereus* AR156, *Bacillus subtilis* SM21, and *Serratia* sp. XY21 increased leaf proline contents three- to fourfold relative to untreated controls. This finding suggested that the increased leaf proline contributed to drought tolerance from over-dehydration. A complementary field and greenhouse experiments in chick pea showed extensive outcomes as compared to control with a combined application of *Mesorhizobium* sp. BHURC02 and *B. megaterium* (Verma et al. 2012). Generally, all findings suggested an improved growth and yield of plants upon microbial inoculation; more importantly co-inoculation is the prominent solution.

7.9 Challenges and Opportunities in Using Rhizobial Inoculants

Inoculation of legumes with rhizobia inoculants has been more often used than BNF technology in agriculture, but in most African countries which include Ethiopia, this technology is not well established (Deshwal and Chaubey 2014). The commercial production of inoculant in Africa faces various challenges. Production and marketability of bioinoculants are highly small, due to the fact that legume production is an emerging industry. Since the product consists of bio-tools with exceedingly short shelf life, the production process and technologies and environment need to satisfy strict criteria to produce a quality product. Moreover, transport and storage facilities are required to maintain the quality of the product. The expense for the components has been limited which helps keeping the price for inoculants low. However, considerable investments either from the government or NGO are required for the production facility and equipment. Distribution is a challenge, particularly if the smallholder farmer community has to be served, taking small trading volumes required storage facilities into account. The economics values of rhizobium biofertilizer utilization in small-scale farming systems in Zimbabwe and the role for policy have indicated that a break-even point (where total revenue equals total cost) is reached at the production of around 40,000–50,000 units (100 g). The inconsistency laboratory and field outcomes are more compounded due to more than a few abiotic stresses that succeed under field conditions for a microbial inoculant to show the desired effect. Such problems can be overcome by the aid of sound screening program for efficient stress-tolerant and phytobeneficial PGPRs (Gupta et al. 2015). One of the principal limiting factors in widespread use of PGPRs is their selectivity. The available technologies for inoculant production and application have been abundantly reviewed in the past. An important point to underline is the relatively small quantities of inoculation technologies emerging from basic research on the genetics of rhizobia and the mechanisms of the legume-*Rhizobium* symbiosis. There is the possibility to get more productive, efficient, and competitive N_2-fixing bacteria.

7.10 Conclusion and Future Prospects

The world's ecosystems are affected with various processes carried out in/on the soil. Climate change and associated environmental stresses with soil acidity have been taking the prior position. The negative effect of synthetic agrochemicals on environment and human health shifts an urgent interest in improving and utilization of rhizospheric microbial populations. These lead bioinoculants the first choice in the current scenarios of chemical fertilizer and pesticide effects. Legumes and other plant inoculation with improved phytobeneficial microbes have been helpful for farmers specifically in stressed environments. Rhizobia and PGPR are reported to influence crop growth, yield, and nutrient uptake by different mechanisms. They fix nitrogen; help in promoting free-living nitrogen-fixing bacteria; increase supply of other nutrients, such as phosphorus and iron; produce plant hormones; enhance other beneficial bacteria; control bacterial and fungal diseases; and help in stress tolerance in plants. Since most single inoculant might in part account for the recorded inconsistencies in field application, the possible means to overcome this problem has been via co-inoculation. Hence, the better understanding of rhizobial physiological and molecular responses to different intrinsic and extrinsic stresses factors is very important to improve crop production by harnessing biological nitrogen fixation process.

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Heavy Metal Stress and Tolerance in Plants Mediated by Rhizospheric Microbes

8

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Abstract

The environmental contamination has become a serious issue in recent times due to human engagements, such as application of pesticides, chemical preservatives, mining, coal combustion, etc. These anthropogenic activities have imposed escalated heavy metal concentrations in water, soil, and air. Specifically, heavy metal pollution of soils causes numerous environmental complications and imparts detrimental effect on living organisms including microbes, plants, and animals. In order to adapt, tolerate, and survive in these adverse situations, plants have evolved with multifaceted molecular and biological mechanisms. Though plants possess many defensive mechanisms to overcome heavy metal intoxication, these strategies of tolerance may not be effective beyond certain limit. Hence, plants will be at the risk of survival. Some of the methods used for removing heavy metals from soil include soil washing with physical or chemical methods; excavation, i.e., the physical elimination from polluted sites; and in situ fixation, the addition of chemicals to stabilize and alter heavy metals to a state that cannot be absorbed by plants. Still, these chemical and physical techniques are not very efficient and the process is expensive. Alternatively, the biological ways of cleaning the contaminated areas have gained more importance in recent times. These

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approaches include the phytoremediation and the application of rhizospheric microorganisms to clean up the soil. Particularly, rhizospheric microorganisms have the ability to shield the plant from heavy metal stress. To be specific, microbes have the molecular machinery to adopt and can survive even in the existence of toxic levels of heavy metals. In the present chapter, the knowledge of heavy metal toxicity and its remediation using microbes is discussed and the utilization of soil microbes for combating the heavy metal stress in plants is also highlighted.

Keywords
Abiotic stress · PGPRs · Plant-microbe association · Stress tolerance · Remediation

8.1 Introduction

Plants have a dynamic driving force to accomplish the essential safeguarding processes including cellular biosynthetic processes and transport to sustain its characteristic structure and regulate the growth. This maintenance process of a system results in a stable condition, called homeostasis. Any variation in the environment that results in altering the plant homeostatic status is referred to as plant stress condition. The plant physiology is destructively affected by plant stresses, because of the rapid transition from an ideal environmental setting to disrupted homeostatic state. Plant stresses can be categorized into two types, namely, abiotic and biotic stresses. Abiotic stresses can be well-defined as the undesirable influence of inorganic or nonliving factors on plants. This may include physical factors like temperature, light, etc. or chemical factors like salinity, heavy metal compounds, etc. On the other hand, biotic stresses are described as the harmful impact of any living factors on plants, such as fungi, bacteria, etc. Plants are challenged to different abiotic stresses, like salinity, low water availability (drought), extreme temperatures (cold, frost, and heat), excessive water (flooding), mineral deficiency, and heavy metal toxicity (Sha Valli Khan et al. 2014). This negative impact of abiotic stress will bring changes in the plant growth, metabolism, productivity, and development and also leads to the death of plants. Likewise, biotic stresses include all damages done by any organisms including microbes (bacteria, fungi, and viruses), parasites, insects, weeds, etc. In agriculture, the limited productivity due to the stress-related changes will result in economic loss for the farmers, where the crop production is reduced by almost 70% (Boyer 1982; Saxena et al. 2013).

In plants, abiotic stress has primary effects and secondary effects. Some of the primary effects include reduced water potential which leads to cellular dehydration, causing alterations in both structural and biochemical activities of cells. This leads to subsidiary effects to weaken the metabolic activity and cause cytotoxicity by inducing reactive oxygen species (ROS) production. Also, the cellular integrity is disrupted, causing cell death. The stress on plants leads to growth suppression by inhibiting protein synthesis and increasing protein folding and processing. The plant stress prevents seed germination, retards development, and reduces nodule formation and crop yield. Further, a significant reduction of seed germination, seedling development, plant height, leaf area, leaf weight, photosynthesis rate, and stomatal conductance and poor vegetative and reproductive growth are observed. Under the anaerobic condition, Fe toxicity is usually very high and leads to increased polyphenol oxidase activity, which leads to the production of oxidized polyphenols. Also, it causes leaf bronzing and reduced root oxidation power, which adversely affects the integrity of the cytoplasm (Farid et al. 2013). Increased levels of heavy metals will generate ROS like hydroxyl free radicals, superoxide free radicals, and non-free radical species like singlet oxygen and hydrogen peroxide that results in the oxidative stress (Zengin and Munzuroglu 2005).

Plants have established different machineries for the acclimation and adaptation in such adverse environmental conditions. Such adverse conditions induce a variety of genes, which are thought to regulate stress tolerance and control the gene expression through signal transduction pathways (Xiong et al. 2002). Plants can overcome drought condition by making use of harmonious solutes and organic composites, which are having high solubility and assist in the adjustment of osmotic condition. This will certainly help in the prevention of protein and membrane denaturation. Plants accumulate many amino acids along with amides and imino acid to survive under abiotic stresses, such as drought and salinity (Koyro et al. 2012). Another unique and overlapping signal is the hyperosmotic signal, which leads to the accumulation of abscisic acid (ABA), a phytohormone. ABA stimulates several adaptive responses in plants under stress conditions (Zhu 2016).

Many microbes have a vital role in inducing stress-tolerant response in the plants. One of the major groups includes the beneficial soil microorganisms that are linked in the process of organic matter decomposition in soils making nutrients available for plants. These microorganisms have the capability to encourage growth of plants under a stressed condition. Among these microbes, plant growth-promoting rhizobacteria (PGPRs), arbuscular mycorrhizal fungi (AMF), etc. are very significant ones. They remain associated with plant roots and are involved directly or indirectly in a number of mechanisms to overcome the stress. Microbes, such as AMF and *Trichoderma* species, accelerate seed germination and enhance seedling vigor to ameliorate abiotic stresses like water, salinity, and heat. Many microbes are known to secrete many phytohormones, mainly indole acetic acid. In addition, microbes also produce plant-specific metabolites or volatile compounds, maintaining the homeostasis, promoting nutrition uptake, promoting antioxidant mechanisms, etc. (Mishra et al. 2017).

High concentrations of heavy metals cause either a decrease or total destruction of all metabolic activities in plants. Plants may possess many defensive mechanisms to overcome heavy metal intoxication. However, beyond certain limit these strategies of tolerance may not be effective, and hence plants will be at the risk of survival (Clemens and Ma 2016; Mishra et al. 2017). Therefore, it is essential to eliminate the accretion of heavy metals in soils to allow plants and other living entities to perform their normal physiological activities to survive in the environment. Some of the methods used for removing heavy metals from soil include soil washing with physical or chemical methods; excavation, i.e., the physical elimination from polluted sites; and in situ fixation, the addition of chemicals to stabilize and alter heavy metals to a state that cannot be absorbed by plants. Still, these chemical and physical techniques are not very efficient and the process is expensive (Schnoor 1997; Mishra et al. 2017). Considering this, cost-effective and effective environmentally friendly approaches should be encouraged to clean up heavy metals in the polluted soils. Alternatively, the biological ways of cleaning the contaminated areas have gained more importance in recent times (Gavrilescu 2004; Wuana and Okieimen 2011; Mishra et al. 2017). These approaches include the phytoremediation, i.e., growing plants to decrease the heavy metal levels in the soil, and the application of rhizospheric microorganisms to clean up the soil. Further, rhizospheric microorganisms have the capability to shield the plant from heavy metal stress. In specific, microbes have the molecular machinery to adopt and can survive even in the existence of toxic levels of heavy metals. In the present chapter, the knowledge of heavy metal toxicity and its remediation using microbes is discussed and the utilization of soil microbes for combating the heavy metal stress in plants is also highlighted.

8.2 Heavy Metal Toxicity in Plants

Anthropological activities of man like industrialization, urbanization, mining, and modern agricultural practices have a detrimental effect on the environment. Soil is the basic and most essential part of the ecosystem supporting the living organisms. The accumulated heavy metal has become the major contaminant in the soil, thus affecting the survival of living beings (Shahid et al. 2012). The soil is receiving a significant amount of these pollutants from various sources throughout the world every year (Wannaz et al. 2012). Some of the heavy metals like Zn, Cu, Co, Mn, and Ni are known to be very important elements for the fundamental biological activities involved in the plant growth development. But, increased concentration of these metals together with other extremely lethal heavy metals, such as Pb, As, Cd, Cr, Hg, and Be, will decrease the crop production to a greater extent by causing morphological abnormalities and altering the metabolic pathways (Salla et al. 2011; Fig. 8.1). The Agency for Toxic Substances and Disease Registry has classified Pb, As, Hg, and Cd as the extreme toxic metals.

Heavy metals have an adverse effect on plants as they inhibit the growth, alter the physiology and metabolism, and inhibit photosynthesis, respiration, and efflux of cations. They affect the plant physiology and metabolic activities by altering activities of key enzymes like phosphoenolpyruvate carboxylase (PEPC) and ribulose 1,5-bisphosphate carboxylase (RuBisCO). Heavy metals disrupt redox homeostasis by encouraging the production of excessive ROS, such as singlet oxygen ($^1O_2$), hydroxyl radical ($OH^\bullet$), superoxide (O_2^-), and hydrogen peroxide (H_2O_2) (Ashfaque et al. 2016). To survive under the heavy metal stress condition, few plants have developed a detoxification mechanism, which is mainly based upon the chelation and subcellular compartmentalization. However, only 20–30% of the plants have genetic potential to overcome the heavy metal stress. The crop production under such a stressed environment is made possible by many microorganisms like PGPRs, AMF, and other rhizospheric microbes. These microbes mitigate the metal ion

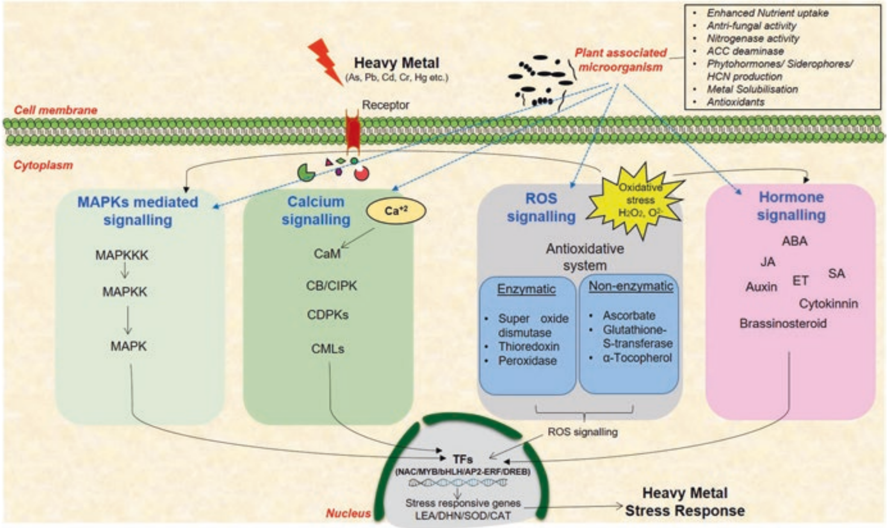

Fig. 8.1 Schematic presentation of signaling pathways between the plant, associated microbes, and heavy metals

toxicity by binding them and transporting them into the cell. In soils, microorganisms have the ability to change the mobility, metal speciation, toxicity, and dissolution and deteriorate them (Ehrlich 1997).

8.2.1 Toxic Effects of Arsenic (As) in Plants

Arsenic (As) is a noxious metalloid, which occurs naturally via volcanic eruption along with Pb, Ag, Zn, and Cu and erosion of rocks (Sharma 2012). It enters the environment by anthropological activities, such as the use of pesticides and chemical preservatives, mining, coal combustion, and smelting processes (Tiwari and Lata 2018). The use of groundwater contaminated with As for irrigation affects the crop production. It enters the food chain by accumulating in different plant tissues and grains (Verma et al. 2016). It is easily taken up by plants, because it is an analogue of phosphate, and so it competes to bind to the carrier in the plasmalemma of plants (Meharg and Macnair 1992). Inorganic arsenate As(V) and arsenite As(III) are the two forms, which are existing in the environment. The United States Environmental Protection Agency (USEPA) has valued both these two forms as poisonous, stated as the chief environmental pollutants (Tripathi et al. 2007; Verma et al. 2016). Arsenic is not necessary and mostly toxic to plants (Finnegan and Chen 2012). In macroalgae and phytoplankton, As undergoes transformation to less phytotoxic As species. They are converted to dimethylarsinic aid, monomethylarsinic acid, and arsenite. After methylation, these forms are metabolized to form arsenosugars and organophospholipids (Yadav 2010). Many terrestrial plants are known to overcome the toxicity of arsenate (Yadav 2010). Studies have shown that As induces oxidative stresses openly by producing ROS during the conversion of its valence forms. Also, it inactivates antioxidant molecules by binding with their -SH groups of enzymes that are linked to the tricarboxylic acid cycle and glycolysis pathways. Further, study reports have stated the presence of truncated levels of methylated As species like dimethylarsinic acid and monomethylarsinic acid in plants (Sharma 2012). As-intervened oxidative stresses cause physiological, molecular, and cellular instabilities in numerous plants. It impedes the respiratory process by binding to vicinal thiols in 2- oxoglutarate dehydrogenase and pyruvate dehydrogenase. Also, it acts as a mutagen by bringing intrachromosomal homologous recombinations (Helleday et al. 2000; Yadav 2010; Talaat and Shawky 2017; Abbas et al. 2018). Numerous plant species have been recognized with As tolerance through different mechanisms. For example, As-tolerant grasses overcome toxicity by suppressing high-affinity phosphate/As^{5+} uptake system (Meharg and Macnair1992). This is attained by a particular gene that encodes for protein that suppresses phosphate/As^{5+} transport system and reduces the influx of As to a reduced level that can be easily detoxified by plants (Yadav 2010). In the same way, other mechanisms have been established by plants to counterbalance As-persuaded oxidative stresses. Some of the major mechanisms include the stimulation of enzymatic antioxidants like ascorbate, glutathione, and carotenoids in ferns and some higher plants (Sharma et al. 2007). Some of the vital enzymes involved in the process of mitigating ROS induced by As uptake include ascorbate peroxidase, superoxide dismutase, catalase, glutathione S-transferase, glutathione reductase, etc. (Eick et al. 1999). Additionally, proline as a nonenzyme antioxidant and osmoprotectant is mostly accumulated in As-stressed plants. In specific, it acts as a plant cell wall plasticizer to sustain hydration required for the regular activity of a cell. Further, it guards plants against ROS-intervened cellular damages (Abbas et al. 2018).

8.2.2 Toxic Effects of Lead (Pb) in Plants

Lead (Pb) is one among the main disseminated harmful elements in the water and soil sources. Besides the natural weathering process, other major sources of Pb include exhaust emissions of vehicles, industries, mining, smelting of Pb ores, storage battery, explosives, fertilizers, and additives in gasoline. Pb is usually amassed in the outer regions of soils and its levels decline with the soil depth (de Abreu et al. 1998). Pb is nonbiodegradable and possesses many detrimental effects on the living organisms (Bradham et al. 2006; Pehlivan et al. 2009). Pb is readily taken up by plants in significant quantities; however it is greatly restricted to be translocated to aboveground plant parts (Ashraf et al. 2017). In soil, Pb absorption follows the Langmuir equation. Further, the Pb absorption significantly increases when the soil pH is between 3.0 and 8.5. However Pb is tightly bound to the colloidal material in the precipitated form, which reduces its uptake by plants. Other mechanisms that prevent the uptake of Pb are extracellular precipitation, mucilage sheath at the root surface, and ion exchange sites on the cell wall (Jarvis and Leung 2002). The adverse effects of Pb include the changes in morphological features of plants and inhibition of plant growth and its photosynthetic process. It impairs biological processes like cell division, seedling development, seed germination, root elongation, transpiration, and chlorophyll biosynthesis (Pourrut et al. 2011; Kumar et al. 2017). In addition, Pb causes the suppression of enzymatic activities, water imbalances, membrane permeability alterations, and distraction of mineral nourishment (Sharma and Dubey 2005). Pb toxicity leads to the inhibition of ATP production and induces lipid peroxidation, enzyme inhibition by binding to sulfhydryl groups, and DNA damage by ROS over production (Yadav 2010).

8.2.3 Toxic Effects of Zinc (Zn) in Plants

Zinc (Zn) is a crucial trace element needed for many physiological events in plants (Sagardoy et al. 2009). It does not take part in redox activity. It is one of the constituents of many coenzymes and an indispensable component of special proteins, known as zinc fingers, which binds to DNA and RNA to regulate their functions (Gupta et al. 2012). The amounts of Zn in unpolluted soil are lower than 125 ppm, which is sufficient enough to support the plant growth (Ebbs and Kochian 1992). However, its increased concentrations, i.e., 150 to 300 mg/kg, are regarded as contamination and are toxic to the plant (de Vries et al. 2007). Its sources of contamination include fertilizers, mining, urban composts, sewage sludge, emissions from waste incinerators, industries, and many other human activities (Van Assche and Clijsters 1986; Wuana and Okieimen 2011). Zn toxicity inhibits many plant metabolic functions resulting in retarded growth of plants and causing senescence and chlorosis in the younger leaves. Also, the increased concentration of Zn leads to Mn and Cu deficiency due to hindering of the transmittance of these micronutrients from root to shoot (Ebbs and Kochian 1992). Further, Zn can disturb the activities in soils and negatively impact on the functioning of earthworms and microbes and hence retard the organic matter breakdown (Wuana and Okieimen 2011; Richardson et al. 2018).

8.2.4 Toxic Effects of Chromium (Cr) in Plants

Chromium (Cr) is another copious metal in the crusts of earth. It is one of the imperative environmental contaminants found in the atmosphere, because of their increased uses in industries. Cr accumulates in groundwater, soil, and sediments (Shanker et al. 2005). According to an estimate, Cr accumulation in freshwater bodies is about 3550 mt worldwide due to anthropogenic discharges (Yadav 2010). Cr is present in two stable oxidation states, namely, trivalent chromium (Cr^{3+}) and hexavalent chromium (Cr^{6+}), which have differences in their bioavailability, mobility, and toxicity (Panda and Patra 2000). Cr^{6+} forms chromate and dichromate and is highly soluble in water. Hence, it is considered as more toxic than Cr^{3+}, which is less soluble in water, and also it is required in trace amounts as an inorganic nutrient for animals. The Cr uptake mechanisms have been studied in many plants. The uptake of Cr^{6+} depends on metabolic energy, while Cr^{3+} does not (Skeffington et al. 1976). After the uptake, Cr is moved in the xylem of the plants. It is mostly accumulated in the roots; however it is also accumulated in low quantities in the vegetative and reproductive organs of the plants. The reason for the high accumulation in roots is due to the fact that Cr is immobilized in vacuoles of the root cells to mitigate its toxicity (Shanker et al. 2004). The effects of Cr include reduction of germination percentage and bud sprouting; decreased root length, diameter, and number of root hairs; plant height reduction; and reduced leaf number (Anderson et al. 1973; Sharma and Sharma 1993; Rout et al. 2000; Panda and Patra 2000; Suseela et al. 2002; Sharma et al. 2003). All these above effects are due to the generation of ROS like H_2O_2 and O_2 (Panda and Patra 2000; Shanker et al. 2005; Stambulska et al. 2018).

8.2.5 Toxic Effects of Mercury (Hg) in Plants

Mercury (Hg) is also the major pollutant in the ecosystem and its dispersal on the surroundings is measured to be a severe ecological issue for its persistent nature (Liu et al. 2010). It is found in several physical and chemical forms like elemental Hg; inorganic Hg, i.e., (Hg^{2+}), mercurous chloride, or calomel Hg_2Cl_2; and organic Hg, like CH_3Hg (Zahir et al. 2005; Clarkson and Magos 2006). Soil is contaminated by Hg as a part of fertilizers, lime, sludge, and manures. Plants uptake Hg in the same process as micronutrients, competing with these elements for absorption; Hg preferentially binds with sulfur and nitrogen ligands and enters through ionic channels (Blazka and Shaikh 1992). The uptake can be reduced when the soil's pH is high or in the abundance of lime and salts (Patra et al. 2004). The effects of Hg on plants are as follows: important molecules like enzymes and polynucleotides are blocked, the permeability of cell membrane is changed, and antioxidant defense system is affected, like nonenzymatic antioxidants glutathione, nonprotein thiols, ascorbate peroxidase, superoxide dismutase, and glutathione reductase (Ortega-Villasante et al. 2005). It inhibits seed germination and elongation of root and reduced photosynthesis and transpiration rate. The uptake of Hg is known to cause genotoxicity by binding to the DNA which results in chromosomal damage, chromosomal aberrations, spindle alterations, and sister chromatid exchange (Patra et al. 2004).

8.2.6 Toxic Effects of Aluminum (Al) in Plants

Aluminum (Al) is the third most copious metallic element in soils and also in air and water. A large amount of Al is incorporated into alumina silicate soil minerals, and only small quantities appear in soluble forms capable of playing a major role in biological system (May and Nordstrom 1991). Diverse forms of Al occur in the soil solution, i.e., $Al(OH)_2^+$ and $Al(OH)^{2+}$ at pH 4–5, Al^{3+} at pH 5.5–7, and $Al(OH)_4$ at pH 7–8. Other complex ions, such as the K-Al13 polymer and Al^{3+}, are also almost toxic in nature. It has been estimated that around 50% of the cultivated land areas are harmfully affected by the toxicity of Al because of the acidic soil. The uptake of Al from the soil follows transpiration stream via the xylem into leaf mesophylls of plants (Haridasan et al. 1986). A high concentration of Al occurring in the plant bark indicates a probable transport pathway via the phloem tissues. Al is very reactive with several prospective binding sites, such as the surface of plasma membrane, the cell wall, the nucleus, and the cytoskeleton. Plant roots are the most likely affected regions of Al toxicity. In specific, Al inhibits root growth elongation by blocking cell division. Thus, roots become stunted, brittle, and physically damaged. It alters the plasma membrane by interacting with lipids and indirectly prevents the cell division and elongation of roots (Delhaize and Ryan 1995). Al toxicity disrupts the structure of the cytoskeleton, photosynthesis, and chloroplast architecture. Binding to DNA will condense and inhibit cell division and transcription (Matsumoto 1988). It affects the physiological functions by releasing ROS and suppresses the mitochondrial respiratory functions (Panda et al. 2008).

8.3 Microorganisms and Bioremediation of Heavy Metals

An environmental problem due to the heavy metal pollution and their negative impact in agriculture has been a serious issue. Biologically, heavy metals may not be destroyed; however they can be altered from one organic complex to another form (Garbisu and Alkorta 2001). Some approaches utilized for the remediation include land filling, excavation, acid leaching, thermal treatment, and electro-reclamation. However, they are not preferred due to higher cost and safety concerns. Different methods have been studied for a natural means of bioremediation, which does not have any undesirable effects on the nature and is low cost, hence highly preferred. The utilization of biological mechanisms inherited by soil microbes and plants to eradicate hazardous pollutants has gained more importance in recent times (Ayangbenro and Babalola 2018). Microbial inoculants including endophytic microbes, mycorrhizae, or PGPRs could safeguard plants to overcome the negative effects of heavy metals in the contaminated soils. The application of green plants to neutralize the heavy metal-polluted sites is recognized as phytoremediation.

8.3.1 Role of PGPRs in Mitigation of Heavy Metal Toxicity

The rhizosphere, an area of soil and plant, inhabits many numbers of microbial species, which play an important role in the bioremediation of heavy metal-contaminated soils. Microbes have an effect on the heavy metal mobility and accessibility to plants via different mechanisms. Bacteria alleviate toxicity effects through immobilization, mobilization, uptake, or transformation of heavy metals through symbiotic or nonsymbiotic associations (Hassan et al. 2017). Many soil microbes inhabit in the rhizospheric soil and have the ability to positively influence plant growth and productivity through the secretion of plant growth hormones and facilitate the uptake of nutrients from soils (Nadeem et al. 2014). PGPRs colonize in the rhizospheric soil or root surrounding and promote plant growth by fixing the atmospheric nitrogen, increasing phosphate solubilization, or secreting phytohormones (Ma et al. 2011). The bioremediation by PGPRs includes various mechanisms, such as chelation, acidification, complexation, precipitation, and redox reaction. The acidification of microenvironment by PGPRs is due to the release of their organic exudates, which in turn will decrease the pH of the soil. This high acidic condition will increase the uptake of many heavy metals by plants. Many bacteria produce organic acids like gluconic, oxalic, acetic, and malic acid that are mainly reported for heavy metal solubilization, where they act as natural chelating agents (Ullah et al. 2015; Mishra et al. 2017). For instance, oxalic and citric acid produced by heavy metal-tolerant *Beauveria caledonica* is reported to solubilize Cd, Cu, Pb, and Zn metals (Gadd et al. 2014). Likewise, chelation leads to biosorption of heavy metals by plants. It has been documented that many metals, including Mn(IV) and Fe(III), can be reduced by metal-reducing bacteria, which uses organic compounds as electron donors (Lloyd 2003). The soil microbes are responsible for mediating the redox reaction having a major effect on transforming a heavy metal to relatively a non-toxic form (Amstaetter et al. 2009). As reported earlier in *Shewanella* and *Geobacter* species, the trans-outer membrane porin-cytochrome protein complex, external membrane c-type cytochromes, and extracellular electron acceptor proteins play a key role in microbe-mediated metal reduction reactions (Shi et al. 2016). Many specific enzymes, such as multicopper oxidases and transcription factor, CopR, released by microbes, are involved in efflux of Cu from cells (Yang et al. 2017; Etesami 2018). Likewise, the enzyme chromate reductase (ChrA) performs the reduction of Cr^{+6} to less toxic Cr^{+3} (Baldiris et al. 2018). A Cr-resistant bacteria, *Cellulosimicrobium cellulans*, can transform toxic Cr^{6+} to nontoxic Cr^{3+} and also has the ability to enhance Cr uptake in green chili shoots and roots (Chatterjee et al. 2009). In mercury toxicity, mercury reductase enzyme reduces Hg^{2+} to less toxic Hg^0 (Naguib et al. 2018). In the As-contaminated soils, Majumder et al. (2013) isolated and identified As-oxidizing bacteria, namely, *Bacillus* sp. and *Geobacillus* species, having the ability to biotransform toxic As^{3+} to less toxic As^{5+}. Rhizobacterium species are reported to improve plant growth and development under metal-stress conditions via both direct and indirect ways (Solano et al. 2008). PGPRs can act in three ways: (1) decreasing the plant pathogens, (2) encouraging nutrient uptake from soils, and (3) producing volatile compounds for the plants (Glick et al. 1998; Zhuang et al. 2007; Khan et al. 2009). Indirect methods include free nitrogen fixation, synthesis of enzymes that can hydrolyze cell wall of fungi and hydrolyze toxins released by pathogens, and helping symbiotic relationship with mycorrhizae and bacteria (Solano et al. 2008). Many numbers of PGPRs are able to modulate plant-soil chemistry through intervening in the methylation process of Pb, Se, Tn, Hg, As, and Sn. These PGPRs have the capability to transfer methyl groups to the heavy metals and form methylated metallic compounds that can be excavated easily in the soil zone (Talaat and Shawky 2017). Biofertilization is the direct plant growth-promoting mechanism in which microbes synthesize phytohormones like indole acetic acid (IAA) (Dimkpa et al. 2009). The growth of *Brassica juncea* was improved by the produced IAA by *B. subtilis* strain SJ-101 in the soil contaminated by Ni (Zaidi et al. 2006). Other microbes tolerant to heavy metals like Cd, Zn, Ni, Cu, and Co also have the capability to produce IAA to rapidly elongate roots in plants like *B. juncea* in contaminated soils (Belimov et al. 2005). Rhizobacteria encompassing 1-aminocyclopropane-1-carboxylate (ACC) deaminase activity (to lower the plant ethylene levels) encouraged heavy metal stress tolerance in addition to plant growth and development (Talaat and Shawky 2017). Likewise, Madhaiyan et al. (2007) have reported that *Burkholderia* sp. and *Methylobacterium oryzae* reduce Ni and Cd stress in tomatoes by plummeting their uptake and translocation. The addition of a consortium of microbes, including *Pseudomonas*, *Bradyrhizobium* sp., and *Ochrobactrum cytisi*, showed resistance to heavy metals and improved plant growth of *Lupinus*. Further, this microbial consortium effectively reduced plant toxicity signs and encouraged metal accumulation in roots and shoots. This effect is correlated to close relationship between endophytic PGPRs and plants (Dary et al. 2010). Studies have reported that As- and Pb-tolerant *Bacillus* spp. and Cd-tolerant *Ochrobactrum* sp. possess many plant growth-promoting characteristics that support bioremediation and growth of a rice cultivar (Tiwari and Lata 2018). Also, Islam et al. (2016) showed that Cu-resistant bacteria with oxidative stress reduction property exhibited increased uptake of copper in lentil plants. *Pseudomonas* sp. (strain CPSB21) resistant to Cr^{6+} was isolated by Gupta et al. (2018) from the tannery effluent adulterated farming soils. It was shown to exhibit oxidative stress tolerance, plant growth-promoting properties, and also effective Cr^{6+} bioremediation. In a study by Franchi et al. (2017), the addition of thiosulfate along with metal-resistant microorganisms improved mobilization and uptake of Hg and As in *Lupinus albus* and *Brassica juncea*. Further, it promoted the bioavailability. Studies also have suggested the possible application of genetically transformed rhizobacteria to plants for in situ bioremediation of metal contaminants (Ullah et al. 2015; Ashraf et al. 2017; Tiwari and Lata 2018). More recently, PGPRs, such as *Pseudomonas fluorescens* strain LMG 2189, *Pseudomonas gessardii* strain BLP141, and *Pseudomonas fluorescens* A506, inoculated to lead-contaminated sunflower plant enhanced growth, physiological activities, antioxidant properties, yield, and proline content and reduced the malondialdehyde content of sunflower.

8.3.2 Role of Arbuscular Mycorrhizal Fungi (AMF) in Mitigation of Heavy Metal Toxicity

Fungal species belonging to different genera *Aspergillus*, *Trichoderma*, *Penicillium*, and *Mucor* are being reported to possess the capability of tolerating heavy metal stresses (Tiwari and Lata 2018). In general, the cell walls of fungi exhibit superior metal binding property because of the occurrence of a negative charge on the functional groups of cell wall components, which include phosphate, carboxylic, sulfhydryl, etc. (Tobin 2001; Ong et al. 2017). Mycorrhizal interactions are reciprocally helpful symbioses of higher plant roots and fungi (Harrison 2005). Their association with plants not only makes available to plants crucial nutrients from soil via uptake by extraradical hyphae but also decreases the uptake of the heavy metals by plants (Joner and Leyval 2001). In a study, AMF encouraged Zn tolerance in plants via uptaking and crystallizing Zn in the cortical cells of mycorrhizal associated roots and fungal hyphae. Thus, transfer of Zn to plant shoot was lessened (Khan et al. 2000; Tiwari and Lata 2018). Similarly, it has been reported that AMF improves Mn and Fe uptake in plants at higher concentration levels. However, AMF decreases the translocation of Mn in shoots and concentrates Fe in roots (Leyval et al. 2002). Some mycorrhizal species, such as *Suillus bovinus* and *Thelephora terrestris*, that are confined to the species like *Pinus sylvestris* help in overcoming Cu toxicity (Hall 2002). In some plants, a type of protein called glomalin, a glycoprotein, is produced by the external mycelium of AMF which has the heavy metal binding sites and helps in heavy metal accumulation (Vivas et al. 2003). AMF-associated sunflower plants accumulated high levels of N/Cd, P/Cd, and S/Cd ratios in plant roots and shoots when compared to control plants without AMF association (de Andrade and da Silveira 2008; Talaat and Shawky 2017). Likewise, AMF-associated plants exhibit a clear defending effect against high levels of Mn in soils. Further, AMF strongly stimulated the growth of *Olea europaea* plant under Mn stress via adjusting phosphate absorption and safeguarding better supply of micronutrients and macronutrients (Bati et al. 2015). The wood-rotting fungi, namely, *Ganoderma aff. steyaertanum* and *Fomitopsis* cf. *meliae*, have been shown to contribute in the transformation of heavy metals into lesser toxic forms, such as copper sulfate to copper oxalate hydrate, zinc sulfate to zinc oxalate dihydrate, lead nitrate to lead oxalate, and cadmium sulfate to cadmium oxalate trihydrate (Kaewdoung et al. 2016). A research study by Coreño-Alonso et al. (2014) shows that *Aspergillus niger* var. *tubingensis* Ed8 interacts with Cr(VI) predominantly in a reduction process and helps in providing tolerance in the Cr-contaminated sites. Likewise, studies have reported that chickpea (*Cicer arietinum*) inoculated with *Trichoderma* sp. ameliorated As-induced stress (Tripathi et al. 2013; Tripathi et al. 2017; Tiwari and Lata 2018).

8.4 Conclusions and Future Prospects

In recent years, the environmental contaminations by heavy metals and their remediation have attained more importance due to the fact that few heavy metals persist in the soil, affecting agricultural productivity. Therefore, many approaches have been effectively used for generating plants, which are capable of growing in heavy metal-polluted soils as well as tolerating metal stresses. In this regard, the use of microbial route to overcome heavy metal stress is highly appreciated as it is an effective, cost-effective, and environmental-friendly approach. PGPRs and AMF assist to promote plant growth via altering bioavailability of heavy metals. As microbes have constructive properties of both plant growth-promoting and heavy metal stress tolerance capabilities, they are widely exploited for the bioremediation of metal-contaminated soils. To further support the process of bioremediation, genetically engineered microbial species have been utilized. Indisputably the bioremediation potential can be improved with the use of these engineered microbes. However, their impact on the environment has to be addressed in order to make use of them in the commercial process. Many research findings have isolated, characterized, and confirmed the potential of rhizospheric microbes to overcome plant abiotic stresses; however, a detailed knowledge on the regulatory networks involving plant-linked microbes in overcoming heavy metal stress is yet to be understood in detail. Hence, there is a need of more studies in this regard to unravel the cross talk between rhizospheric microbial species and metal interactions in various plants. Furthermore, the symbioses between plant and its allied microorganisms in the heavy metal-contaminated soils have to be studied in detail. Though some of the mechanisms of action of bioremediation, including heavy metal transformation, mobilization, and decontamination, have been detailed by previous researchers, a better understanding of them must also be investigated. The use of microbial inoculants to plants under heavy metal stress conditions is being reported to be more effective. Hence, the formulation of bioinoculants that include the already proven metal stress-resistant microbial species may augment tolerance capacity of plant under stress. Also, it could be effective as a feasible approach to improve the productivity of commercial crops under the stressful environments in the near future.

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Use of Nanoparticles in Alleviating Salt Stress

9

Irfan Ahmad and Mohd Sayeed Akhtar

Abstract

Soil salinity is one of the major causes of abiotic stress that limits crop productivity. It also affects nearly one-fifth of the worldwide cultivated lands. The negative effects of soil salinity in plants are related to the specific toxicity of ions, such as Na and Cl, as well as to the low osmotic potential of soil solution, which results in water deficiency in plant cells. These conditions make it difficult for a plant to absorb water from saline soils and/or lead to ionic effect resulting from accumulation of toxic salt ions which leads to the reduced growth rates and productivity. Recently, nanotechnology has gained the attentions of scientists in various disciplines of science and plays a vital role in medicine, industries, agriculture, electronics, energy, and environment. In agriculture, using nanoparticles is expected to improve the crop productivity by enhancing plant nutrition, precision farming, water use efficiency, crop protection against pest and diseases by molecular tools and techniques, and environmental protection. Thus, the aim of the chapter is to provide an update on the use of various types of nanoparticles for alleviating the salt stress and also to understand the mechanism behind it.

Keywords

Abiotic stress · Crop · Soil salinity · Nanoparticles · Nanotechnology

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9.1 Introduction

Salinity of soil is one of the main abiotic stresses limiting the growth of crops (Munns and Tester 2008). The high salt concentration in the root zone can be natural or induced by agricultural activities such as irrigation with low-quality water or the use of certain fertilizers (Bartels and Nelson 1994). Salt-affected lands cover large areas in the world spanning from the irrigated Indo-Gangetic Plain to the Great Hungarian Plain, Israel, China, Russia, and the USA. These salt-laden lands are not only unsuitable for grain-based production but also environmentally vulnerable to further degradation, sometimes irreversible. Several problems such as poor porosity, high sodium concentration, waterlogging, and other hydraulic constraints in the soil make these lands unproductive. Such chemically and physically deteriorated land area reflecting sodicity, salinity, waterlogging, and loss of nutrients has been estimated to be 25.75 million ha (Mha) in India (NRSA 2005; Maji et al. 2010). In India there is 6.75 Mha area under salt-affected soils (saline, sodic, and saline-sodic). There is more than 1.2 Mha sodic land in the Indo-Gangetic region alone, which provides opportunity for bolstering food security. Saline soils have neutral salts, mostly Cl^- and SO_4^{2-}. HCO_3^- may be present but CO_3^{2-} is mostly absent, while sodic soils are capable of alkaline hydrolysis and there is preponderance of HCO_3^- and CO_3^{2-} of sodium. The presence of excessive amounts of Na cations (predominantly in sodic conditions) leads to clay soils becoming solid and impenetrable. The presence of salts in the soil causes a limitation and decline in yield in many regions, in which the salt concentration of the soil solution exceeds 100 mM, inhibiting the growth of plants (Shahbaz and Ashraf 2013). Thus, the aim of the chapter is to provide an overview on the use of various types of nanoparticles for alleviating the salt stresses.

9.2 Effect of Salt Stress on Plant Metabolisms

Due to accumulation of salt in soil, there is a change in physiology and metabolism of plants. It affects germination, seedling growth, vegetative phase, flowering, and fruiting leading to decreased yields and quality of production (Vicente et al. 2004; Parida and Das 2005). Presence of high salt concentrations in soil or water leads to osmotic stress, which is one of the most severe stress factors worldwide, with particular importance for numerous regions located in semiarid or climate zones. In addition to physical effects of soluble particles limiting water uptake by roots, the salinity effects are associated also with toxicity of individual ions and nutritional imbalance or interactions of these factors (Ashraf and Harris 2004). Excess salt induces osmotic and ionic stress (Yan et al. 2015). The fast response to salt stress is the slowdown of leaf expansion that ceases at high concentrations (Wang and Nil 2000) and affects negatively plant growth (Hernández et al. 1995). The reduction in growth has been shown to be correlated with the salt concentration and the osmotic potential of soils (Flowers and Colmer 2015). Sodium transport takes place via the water fluxes through the soil pores and thus highly depends on the local porous structure. On the other hand, the Na cations bind to the clay minerals, and this greatly affects the swelling and shrinking behavior of the soil. Clay swelling and dispersion are the key processes making sodic soils unsuitable for agriculture (Bhardwaj et al. 2008). However, growth reduction occurs in most of plant species, but a level of tolerance or sensitivity varies widely among species. For instance, *Raphanus sativus* plants showed 80% of the growth reduction under salt stress is attributed to loss of leaf area (Chartzoulakis and Klapaki 2000). The action of salinity on the growth leading to both an imbalanced nutritional value of essential ions and a high uptake of toxic ions by the plant (Munns 2002) is connected with stress inducing low osmotic potential of soil solution (Munns and Tester 2008; Yan et al. 2013). Growth reduction in Poaceae can be attributed to an excessive uptake of Na^+ ions (Tester and Davenport 2003; Gu et al. 2016). In tomatoes, salinity significantly reduces the mass of aerial parts, the number of leaves, the height of plants, and the plant root area and length (Mohammad et al. 1998).

9.3 Effect of Nanoparticles on Plants

Nanotechnology has gained the attention of researchers in many disciplines of science although nanoparticles exist already with the beginning of the universe. Scientists expect that nanotechnology will play a crucial and vital role in many fields in our life such as in medicine, industry, agriculture, electronics, energy, and environment (Akhtar et al. 2013; Zhang et al. 2015). In agriculture, using nanoparticles is expected to improve the crop productivity by enhancing plant nutrition, precision farming, water use efficiency, crop protection against predators and diseases, innovative tools for pathogen detection, molecular biology, and environmental protection (Walker 2005; Panwar et al. 2012). Because of their unique physicochemical properties, potential nanoparticles can boost plant metabolism (Giraldo et al. 2014). According to Galbraith (2007) and Torney et al. (2007), engineered nanoparticles are able to enter into plant cells and leaves and also can transport DNA and chemicals into plant cells. This territory of research offers new potential outcomes in plant biotechnology to target specific gene manipulation and expression in the particular cells of the plants. Scientists have increased plants' capacity to harvest more light energy by conveying carbon nanotubes into chloroplast, and furthermore carbon nanotubes could fill in as artificial antennae that enable chloroplast to catch wavelengths of light which isn't in their typical range, for example, ultraviolet, green, and near-infrared (Cossins 2014; Giraldo et al. 2014). The engineered carbon nanotubes also boost seed germination, growth, and development of plants (Lahiani et al. 2013; Siddiqui and Al-Whaibi 2014). Nanotechnology has large potential to provide an opportunity for the researchers of plant science and other fields to develop new tools for incorporation of nanoparticles into plants that could augment existing functions and add new ones (Cossins 2014). In the present review, a discussion has been put forward to understand the role of nanoparticles to alleviate plant oxidative stress induced by salt. Nanoparticles interact with plants causing numerous morphological and physiological changes, contingent upon the properties of NPs. Adequacy of NPs is dictated by their chemical composition, size, surface covering, reactivity, and, in particular, the dose at which they are successful (Khodakovskaya et al. 2012).

Silica is the second most abundant element in the earth's crust and is a beneficial element for plants. Silica also has an important role in plant tolerance to environmental stresses such as salinity stress. Plant photosynthesis also increases by application of silicon which results in leaf number and leaf area increment. Moreover, fresh and dry weight in leaf and root significantly increases by silicon application under salinity stress (Gao et al. 2006). Many researchers have been able to produce silica nanoparticles from natural sources. There have been several reports where Si plays a very important role in alleviating the biotic (diseases and pests) and abiotic (salinity, drought, and metal toxicity) stresses by affecting physical and chemical defense system of plants (Epstein 2009; Ma et al. 2011; Farooq and Dietz 2015). Provisioning crop with the adequate dose of Si is expected to expand the productivity and improve its quality. The normal advantages from the utilization of Si originate from improving water use efficiency in plants by decreasing the evapotranspiration by means of the stomata, expanding the action of some antioxidant enzymes, and supporting plants against diseases by lessening their affectability toward the destructive organisms (Roohizadeh et al. 2015). In order to understand the effect of silica nanoparticles on basil grown under salt stress, Kalteh et al. (2014) performed a pot experiment by considering three levels of salinity stress and three levels of silica fertilizer which includes without silica fertilizer, common silica fertilizer, and silica nanoparticles. A significant reduction in growth and development parameters was observed because of the salinity stress. Leaf dry and fresh weight reduced by increment in NaCl concentration while significantly increased with silicon nanoparticles application. A reduction in chlorophyll content was observed under salinity stress which had been overcome by silicon nanoparticles application. In response to salinity stress, proline content was increased. Moreover, proline increased by silicon nanoparticles which was due to tolerance induction in plants. Silicon nanoparticles application diminished the harmful effects of salinity in basil. In another experiment Qados (2015) carried out a pot experiment in the greenhouse during winter season to investigate the mechanisms that might be involved in the ameliorating effects of nanoSi and Si on faba bean plants grown under salinity stress conditions. The effect of nanoSi and Si on characteristics of cell membrane, chlorophyll a and b, carotenoids, carbohydrates, antioxidant enzymes, free proline, and mineral elements was investigated in NaCl-stressed and NaCl-non-stressed faba bean plants. NaCl treatments caused an increase in proline content, and in some enzyme activities, Chl a and b and carotenoids were decreased. Application of NSi caused a significant increase in the activity of ascorbate peroxidase (APX), catalase (CAT), and peroxidase (POD) in plant leaves, but caused a decrease in the activity of superoxide dismutase (SOD) as compared to unstressed plants. Oxidative damage, created by salinity stress, appeared to diminish as per the expansion in antioxidant enzymes activity under NSi and Si treatments; in this manner tolerance against salt stress was observed. The improvement of salt tolerance resulted from NSi, and a Si treatment was accompanied with improved membrane stability, chloroplast formation, and sugar accumulation. He concluded that nano-silicon treatments can reduce the adverse effects of salinity on *V. faba* plants by enhancing the activity of antioxidant enzymes. Keeping in mind the beneficial effect of silica and nanosilica on plant growth, Abdel-Haliem et al. (2017) examined the impacts of Si ions and silica nanoparticles (both separated from rice straw) on the physiological and biochemical reactions and the expression of the two silicon uptake genes LSi1 and LSi2 in rice under different NaCl concentrations. Results demonstrated that silicon ions altogether weakened the hindering physiological and biochemical impacts of NaCl on plants. This was expected among different reasons to jasmonic acid (JA) signaling. This phytohormone up-directed the expression of the silicon uptake genes in salt-treated plants provided with silica ions, initiated their antioxidant defense systems, and instigated osmolyte production. To exploit the engineered nanoparticles in agriculture sector, Alsaeedi et al. (2017) tested the ability of nanosilica (NS) to ameliorate the detrimental impact of Na^+ with different concentrations on the seed germination and the growth of common bean seedlings. The results proved that Na^+ concentrations had detrimental effects on all measured parameters. When the seeds and seedlings were treated with NS, it showed improvement in growth which resulted in higher values for all parameters. For instance, the addition of NS leads to an increase of the final germination percentage, vigor index, and germination speed for seeds. Although common bean seedlings could not grow at the highest level of Na^+, fortification seedlings with NS helped them to grow well. Shoot and root lengths and shoot and root dry masses are also enhanced. These results proved the importance of using NS to relieve the detrimental effects of Na^+-derived salinity. This finding could be strengthened by low Na content which was estimated in plant tissues in the wake of treating seedlings with 300 mg L^{-1} of NS.

Cerium oxide nanoparticles (CeO_2NPS) are widely used in the production of catalysts, sunscreen creams, microelectronics, and polishing agents due to their unique catalytic and optic properties (EPA 2009). They are additionally utilized as a diesel fuel added substance to expand fuel ignition proficiency and decline diesel soot emissions (Cassee et al. 2011). This last application entails great environmental occurrence and impact of these nanoparticles. Previous studies have demonstrated that CeO_2NPS showed solid impacts on plant health both positively and negatively, contingent on the plant species, exposure concentration, exposure duration, and plant development conditions (Ma et al. 2010, 2016a, b; Wang et al. 2012; Zhao et al. 2014). CeO_2NPS were appeared to improve plant development under certain exposure conditions. Wang et al. (2012) found that irrigation with 10 mg l^{-1} of CeO_2NPS slightly improved tomato growth and yield. While the fundamental components for the diverse effects of CeO_2NPS at various concentrations are not completely comprehended, this might be halfway credited to the duel valance conditions of Ce (Ce^{3+} and Ce^{4+}) on the nanoparticle surface, which makes CeO_2NPS carry on as an antioxidant at specific conditions (Wang et al. 2012) and an oxidative stress inducer at different conditions (Ma et al. 2016a, b). ENPs, for example, cerium oxide nanoparticles (CeO_2-NPs), have a noteworthy effect on plant growth and production. Rossi et al. (2016) examined the physiological and biochemical changes in *Brassica napus* L. (canola) cv. “Dwarf Essex” under synergistic salt stress and

CeO_2NPS impacts. NaCl altogether upset plant development and adversely influenced the physiological processes of canola. Plants treated with CeO_2NPS had higher plant biomass, displayed higher proficiency of the photosynthetic apparatus, and had less stress in both freshwater and saline water irrigation conditions. Overall, their outcomes showed that CeO_2NPS prompted changes in canola development and physiology which enhanced the plant salt stress response but did not totally alleviate the salt stress of canola. Later on, Rossi et al. (2017) investigated the impact of CeO_2NPS on plants grown under various concentrations of salinity and postulated that CeO_2NPS could modify plant root anatomy and improve plant salt stress tolerance. *Brassica napus* was grown under various salt concentrations and treated with CeO_2NPS. Freehand sections of fresh roots were taken every 7 days for 3 weeks, and the suberin lamellae improvement was analyzed under a fluorescence microscope. The outcomes affirmed the theory that CeO_2NPS altered the arrangement of the apoplastic barriers in *Brassica* roots. In salt-stressed plants, CeO_2NPS shortened the root apoplastic barriers which allowed more Na^+ transport to shoots and less accumulation of Na^+ in plant roots. The altered Na^+ fluxes and transport led to better physiological performance of *Brassica*.

Zinc oxide (ZnO) NPs (ZNPs), one of the most frequently used nanoproducts, are used in food packaging and drugs due to their superior antimicrobial efficacy (Brayner et al. 2006; Jones et al. 2008). ZNPs are likewise being as often as possible utilized in sun-protective lotions, wall paints, ceramic manufactures, or sporting goods (Fan and Lu 2005; Singh and Nanda 2014). The increased popularity of using Zn in fertilizers and pesticides is also commissioned due to its natural demand as a micronutrient in the body (Prasad et al. 2012). Moreover, Zn is also an important cofactor in essential biocatalytic enzymes including oxidoreductases, transferases, hydrolases, ligases, and isomerases (Auld 2001). In numerous investigations, expanding proof proposes that zinc oxide nanoparticles (ZNPs) increase plant growth and development. Prasad et al. (2012) in peanut, Sedghi et al. (2013) in soybean, Ramesh et al. (2014) in wheat, and Raskar and Laware (2014) in onion reported that lower concentration of ZNPs exhibited a beneficial effect on seed germination. However, higher dose of ZNPs impaired seed germination. The impact of NPs on germination relies upon centralizations of NPs and fluctuates from plants to plants. de la Rosa et al. (2013) applied different concentrations of ZNPs on cucumber, alfalfa, and tomato and found that just cucumber seed germination was upgraded. Raliya and Tarafdar (2013) reported that ZNPs initiated a significant enhancement in *Cyamopsis tetragonoloba* plant biomass, shoot and root development, root area, chlorophyll and protein synthesis, rhizospheric microbial population, and acid and alkaline phosphatase and phytase activity in the rhizosphere of cluster bean. It is obvious from the correlative light and scanning microscope and inductively coupled plasma/atomic emission spectroscopy that seedling roots of *Vigna radiata* and *Cicer arietinum* absorbed ZNPs and showed better growth of root and shoot length and biomass (Mahajan et al. 2011). Nano ZnO supplemented with MS media promoted somatic embryogenesis, shooting, regeneration of plantlets, and furthermore instigated proline synthesis, the activity of superoxide dismutase, catalase, and peroxidase along these lines enhancing resistance to biotic stress (Helaly et al. 2014). Alharby et al. (2016) examined the effectiveness of the application of ZNPs in the evaluation of mRNA expression of SOD and GPX genes and proteins in tomato germplasm under different treatments of NaCl. Treatments with NaCl suppressed the mRNA levels of superoxide dismutase (SOD) and glutathione peroxidase (GPX) genes in all cultivars, while plants treated with ZNPs in the presence of NaCl showed increments in the mRNA expression levels. This demonstrated ZNPs had a positive response on plant metabolism under salt stress. Predominant expression levels of mRNA were seen in the salt-tolerant cultivars, Sandpoint and Edkawy, while the lowest level was identified in the salt-sensitive cultivar, Anna Aasa. SDS-PAGE indicated clear contrasts in patterns of protein expression among the cultivars. A negative protein marker for salt sensitivity and ZNPs was observed at a molecular weight of 19.162 kDa in cv. Anna Aasa, whereas two positive markers at molecular weights of 74.991 and 79.735 kDa were identified in the tolerant cultivar Edkawy. Similarly Latef et al. (2017) evaluated the role of ZnO nanoparticles in lupine (*Lupinus termis*) plants grown under salinity stress. Salinized plants demonstrated a decrease in plant growth parameters (root length, shoot length, fresh weight, and dry weight) and in the contents of photosynthetic pigments (chlorophyll a and b and carotenoids) and Zn, just as in the activity of catalase (CAT) against control plants. On the other hand, saltiness stress boosted the contents of organic solutes (soluble sugar, soluble protein, total free amino acids, and proline), total phenols, malondialdehyde (MDA), ascorbic acid, and Na, just as in the activities of superoxide dismutase (SOD), peroxidase (POD), and ascorbate peroxidase (APX) in stressed plants over control plants. Nonetheless, seed priming with ZNPs for the most part stimulated growth of stressed plants, which was accompanied by reinforcement in the levels of photosynthetic pigments, organic solutes, total phenols, ascorbic acid, and Zn, just as in the activities of SOD, CAT, POD, and APX enzymes over stressed plants alone. Despite what might be expected, priming with ZNPs caused a decrement in the contents of MDA and Na in stressed plants in respect to salinized plants alone. It is qualified to specify that this enhancement in salt tolerance of plants primed with ZNPs was progressively evident in plants primed with ZNPs3 and grown both in unstressed and stressed regimes. Thus, their findings suggest that seed priming with ZNPs, especially 60 mg L^{-1} ZnO, is an effective strategy that can be used to enhance salt tolerance of lupine plants. Soliman et al. (2015) also performed the experiment to investigate the effect of Hoagland solution containing ZnO and Fe_3O_4 nanoparticles on *Moringa peregrina* grown under different levels of salinity. *Moringa peregrina* plants were grown under different levels of saline water and treated with sprayed Hoagland solution containing different concentrations of ZnO and Fe_3O_4 nanoparticles (NP); the normal Hoagland solution was used as a control. Results showed that salinity levels significantly reduced growth parameters (plant height, root length, number of leaves, number of branches, shoot and root fresh and dry weights). Also, chlorophyll, carotenoids, and crude protein levels decreased; meanwhile proline and total carbohydrate levels, antioxidant nonenzymes (vitamins A and C), and enzymes (POD and SOD) increased. *Moringa* plants treated with Hoagland-containing ZnO and Fe_3O_4 NP demonstrated an improvement in growth parameters either under normal or saline conditions when compared with control. Likewise, spraying plants with Hoagland-containing ZnO and Fe_3O_4 NP brought about significant decrease in Na^+ and

Cl^- and an increase in N, P, K^+, Mg^{2+}, Mn^{2+}, Fe, and Zn, total chlorophyll, carotenoids, proline, sugars, crude protein levels, antioxidant nonenzymes, and enzymes when compared to control, normal Hoagland-sprayed plants. By and large, this enhancement of salt tolerance was extensive in plants sprayed with 60 mg/L ZnO and Fe_3O_4 NP and grown either in saline and nonsaline conditions.

Micronutrients can increase plant resistance to the negative effects of toxic ions. Specifically, higher concentrations of iron in nutritional solutions can compensate for salinity impacts (Uauy et al. 2006). Uauy et al. (2006) reported that iron, zinc, and magnesium spraying over wheat shoots led to their improved growth characteristics. In another study, Maciel et al. (2004) stated that the negative effects of saline could be relieved by the application of iron sulfate. Application of iron nanofertilizer in plants can increase the plant resistance to salinity stress by simultaneously increasing the permeability of the root's selective plasma membrane and decreasing the absorption and accumulation of sodium, which improves the ratio of potassium to sodium in the shoot (Taiz et al. 2015).

Several studies have shown that potassium silicate has a positive impact on plant growth and productivity. It has also been proven that silicon improves plant growth, increases photosynthesis, decreases evapotranspiration, stiffens the leaves, increases the chlorophyll concentration in a given leaf area, and improves the quality of the products (Rodrigues et al. 2009). When deposited inside the cell wall, it combines with calcium and pectin to create a cellulose silicon layer that increases the stability of the cell wall against damage by pathogens. Under saline conditions, potassium silicate heightens the enzymatic activities of antioxidants, thus reducing the permeability of plasma membrane and increasing root absorption of nutrient elements (Liang et al. 2003). Silicon, by both limiting transportation of sodium to leaves and storing the sodium inside the root, can improve plant stability against salinity stress. Furthermore, silicon can reduce the toxic effect of sodium, thus improving plant growth and development by reducing the degree to which it is taken up (Gong et al. 2005). Mozafari et al. (2018) performed an experiment to survey the effect of salinity stress on the biochemical and nutritional properties of grape var. Khoshnaw under in vitro conditions and to consider the effect of iron and potassium silicate nanoparticles in compensating for the effects of salinity stress on this plant. They observed that the application of iron nanoparticles and potassium silicate significantly increased the total protein content and reduced proline, enzymatic antioxidant activity, and hydrogen peroxide. Membrane stability index was reduced, while malondialdehyde content increased under salinity stress. Increase of membrane stability index and reduction of malondialdehyde content were obtained under the application of potassium silicate and iron nanoparticle. It had been observed that iron and potassium silicate decreased the sodium content whereas potassium content was increased under salinity stress conditions. The highest ratio of sodium to potassium was observed in plants under salinity conditions treated with neither iron nanoparticles nor potassium silicate; conversely, the lowest ratio was achieved in plants treated with iron nanoparticles and potassium silicate under non-stress conditions. It was concluded that application of micronutrients can overcome the harmful effects of salinity stress (Table 9.1).

Table 9.1 Effect of various nanoparticles on plant growth and productivity under salinity stress has been listed

Nanoparticles	Salt stress	Plant	Parameters	Result	References
Silica nanoparticles	NaCl	Basil (*Ocimum basilicum*)	Chlorophyll a and b, proline, fresh and dry shoot weight	All parameters gave significant result	Kalteh et al. (2014)
Silicon nanoparticles	NaCl	Faba bean (*Vicia faba*)	Membrane characteristics, photosynthetic pigments, soluble sugars, proline, antioxidant enzymes, nutrient elements	Significant results were observed	Qados (2015)
Silica ions and nanosilica	NaCl	Rice (*Oryza sativa* L.)	The quantification of Na, K, Ca, and Si, estimation of proline content, free amino acid (FAA) content, total soluble carbohydrate (TSC) content, malondialdehyde (MDA) content, plasma membrane permeability (PMP), H_2O_2 content, enzymatic antioxidant system, shikimic acid concentration, phenolic compound, hormone	Ca and K content were increased under silica ion. Proline content, free amino acid content, and total carbohydrate content also increased by silica ion under salt stress. MDA content, PMP, and H_2O content were controlled by silica ion, slight increase in antioxidative enzymatic activities, shikimic acid content decreased, phenolic compounds content increased, hormone content amplified	Abdel-Haliem et al. (2017)
Silica nanoparticles	NaCl	Common bean (*Phaseolus vulgaris*)	Seed germination percentage, shoot and root length, fresh and dry mass, sodium, potassium, and silica content	Beneficial effects on all measured parameters	Alsaeedi et al. (2017)

(continued)

Table 9.1 (continued)

Nanoparticles	Salt stress	Plant	Parameters	Result	References
Cerium oxide nanoparticles (CeO_2-NPs)	NaCl	*Brassica napus* L. (canola) cv. “Dwarf Essex”	Growth parameters, leaf pigments, chlorophyll fluorescence, proline, photosynthetic responses, mineral nutrients, cerium uptake	Improved the plant salt stress response but did not completely alleviate the salt stress of canola	Rossi et al. (2016)
Cerium oxide nanoparticles	NaCl	*Brassica napus* L.	Dry mass, concentration of sodium and cerium in tissues, chlorophyll fluorescence, root anatomy	Plant dry mass showed no significant effect, formation of apoplastic barrier, significantly higher values of ratio of variable fluorescence to maximum fluorescence (Fv/Fm), increase in sodium concentration of leaves and roots	Rossi et al. (2017)
ZnO nanoparticles	NaCl	Tomato (*Lycopersicon esculentum* Mill)	mRNA levels of superoxide dismutase (SOD) and glutathione peroxidase (GPX) genes	Increments in the mRNA expression levels	Alharby et al. (2016)
ZnO nanoparticles	NaCl	Lupine (*Lupinus termis*)	Growth traits, photosynthetic pigments, organic solutes (soluble sugar, soluble protein, total free amino acids, and proline), total phenols, malondialdehyde (MDA), antioxidant enzyme activities, ascorbic acid, Na and Zn contents	Stimulated growth of stressed plants, reinforcement in the levels of photosynthetic pigments, organic solutes, total phenols, ascorbic acid and Zn, as well as in the activities of SOD, CAT, POD, and APX enzymes, decrement in the contents of MDA and Na	Latef et al. (2017)

ZnO and Fe_3O_4 magnetic nanoparticles	Synthetic seawater salt	*Moringa peregrina*	Growth parameters, leaf pigments and total carbohydrates, macro- and micronutrients and crude proteins, antioxidant nonenzymes and enzymes	Parameters studied were found to be significantly promoted	Soliman et al. (2015)
Iron nanoparticles	NaCl	Grape	Proline and total protein content, malondialdehyde (MDA) content, H_2O_2 content, peroxidase activity (POD), ascorbate peroxidase activity (APX), superoxide dismutase activity (SOD), sodium and potassium content	Increased the total protein content and reduced proline, enzymatic antioxidant activity and hydrogen peroxide, increase of membrane stability index and reduction of malondialdehyde content, lower the sodium content, and increase the potassium content	Mozafari et al. (2018)
Nitric oxide chitosan nanoparticles	NaCl with mercaptosuccinic acid	*Zea mays*	S-Nitrosothiol content in the leaf, physiological parameters, growth analysis	Higher leaf S-nitrosothiols content, increase in photosystem II activity, chlorophyll content, and growth of maize plants	Oliveira et al. (2016)

Nitric oxide (NO) is a gaseous signaling molecule involved in several processes of plant growth and development, as well as in plant response to abiotic stresses (Baudoiun and Hancock 2013; Simontacchi et al. 2015; Farnese et al. 2016). Exogenous NO application has been shown to mitigate the adverse effects of salt stress in diverse plant species (Zhang et al. 2006; Lu et al. 2011; Chen et al. 2014; Manai et al. 2014; Du et al. 2015; Ahmad et al. 2016; Kong et al. 2016). The involvement of NO in response to salinity has been further substantiated by the higher sensitivity of NO-deficient mutants to salt stress (Zhao et al. 2007; Li et al. 2016). In salt-stressed plants, NO modulates gene expression and protein function, inducing the antioxidant defense system, chlorophyll biosynthesis, osmolyte accumulation, and H^+-ATPase activity (Zhang et al. 2006; Lu et al. 2011; Ahmad et al. 2016; Tanou et al. 2012; Camejo et al. 2013). NO has also been shown to reduce the negative effects of salinity on photosynthesis and the growth of plants subjected to salt stress (Zhang et al. 2006; Ahmad et al. 2016; Tanou et al. 2012), thereby emerging as a molecule with potential uses in agriculture (Seabra et al. 2014). However, the direct treatment of plants with NO is technically difficult, given the gaseous nature of NO (Vitor et al. 2013). Additionally, NO has a short in vivo half-life (1–5 s), rapidly reacting with oxygen and cellular components, which makes necessary a constant delivery of NO to the tissues (Seabra and Duran 2010; Seabra et al. 2014, 2015a, b, c). Low-molecular-weight NO donors, such as S-nitrosothiols (RSNOs) and sodium nitroprusside (SNP), have been widely used for the investigation of biological functions of NO both in plants and in animal models (Ahmad et al. 2016; Li et al. 2016; Seabra et al. 2014a; b, 2015a, b, c; Jamali et al. 2015; Silveira et al. 2016; Singh and Bhatla 2016; Pereira et al. 2015). Oliveira et al. (2016) have successfully encapsulated low-molecular-weight NO donors in chitosan nanoparticles (CS NPs) for different biomedical applications, including antimicrobial activities against resistant bacteria (Cardozo et al. 2014) and protozoa (Seabra et al. 2015b). They reported the synthesis and characterization of CS NPs containing S-nitroso-mercaptosuccinic acid (S-nitroso-MSA), a low-molecular-weight NO donor that belongs to the class of RSNOs. S-Nitroso-MSA-CS NPs were used as spontaneous NO donors in maize plants submitted to salt stress. For this, the NPs were synthesized through ionotropic gelation process, and mercaptosuccinic acid (MSA), the NO donor precursor, was encapsulated into CS NPs. Free thiol groups of MSA-CS NPs were nitrosated, prompting S-nitroso-MSA-CS NPs (NO-releasing NPs). The integration of S-nitroso-MSA into CS NPs permitted a continuous NO release. Treatments of salt-stressed maize plants with S-nitroso-MSA-CS NPs brought about a higher leaf S-nitrosothiol content contrasted with that of free S-nitroso-MSA. Besides, S-nitroso-MSA-CS NPs were more proficient than was the free NO donor in the enhancement of the harmful impacts of salinity in photosystem II activity, chlorophyll content, and development of maize plants in light of the fact that the defensive activity of the nanoencapsulated S-nitroso-MSA was accomplished at lower dosages. In general, these outcomes exhibit the positive effect of S-nitroso-MSA nanoencapsulation in expanding NO bioactivity in maize plants under salt stress.

9.4 Conclusions and Future Prospects

Nanoparticles had several novel applications in various fields of science due to their unique properties. The effect of nanoparticles on plant varies from plants to plants and also depends on their mode of application, size, and concentration. This research on NPs, essentiality for plants, is in the beginning; more rigorous works are needed to understand physiological, biochemical, and molecular mechanisms of plants in relation to NPs. Likewise, more examinations are expected to investigate the mode of activity of NPs, their interaction with biomolecules, and their impact on the regulation of gene expressions in plants.

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10

Soil-Plant and Microbial Interaction in Improving Salt Stress

Hera Nadeem and Faheem Ahmad

Abstract

Soils are complex mixtures of minerals, water, organic matter, and countless organisms that are the decaying remains of living beings and together support life. Along with compounds such as amino and organic acid, some fascinating natural and synthetic metabolites are common moieties found in soil. One of the major and dominant concerns for the development and maintenance of the agriculture system world is saline soil, as salt-affected area becomes unproductive and hence worthless for the agro-industries. Salinity is lowering the yield of the crop by discouraging the overall metabolism of the plants. To overcome this problem and to provide sustenance to plant vigor and soil health, vital constituent of soil microbiota-specific plant growth-promoting rhizobacteria (PGPR) and mycorrhizae plays the crucial role. Besides eliciting plant defense reactions against various soilborne pathogens, the PGPRs have also the aptitude to produce phytohormone, enzyme acetyl-CoA carboxylase deaminase, solubilize and bind nutrients, and, therefore, assist plants to acclimatize with various environmental stresses. Osmotic stress and noxious ion produced due to salinity induce the unacceptable plant development and reduce soil microbial activity. The microbes have the potential to produce osmolytes, which may neutralize the severe effects of osmotic stress and help plants to regain cell turgor and metabolism. The collaboration of plant, stress-tolerant microbe, and organic amendment provides an auspicious ambiance for the expansion of beneficial microbes which in return amplify plant growth in disturbed agroecosystem. For managing disrupted agricultural land due to the climate change resilience, efficacious approach among others is taking advantage of the plant-microbe guild having accordant microbial agents with the agricultural land use pattern. Thus, the aim of this

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chapter is to provide an overview of the soil, plant, and microbial interactions in improving the salt stress conditions.

Keywords

PGPR · Plant-microbe interactions · Salinity · Salt tolerant · Sustainable agriculture

10.1 Introduction

Soil salinity is described as the high amount of salt content in the soil (Shrivastava and Kumar 2015; Asfaw et al. 2018). The high osmotic pressure created by the accumulation of salts in the soil moisture of the rhizosphere restricts water uptake and absorption of crucial nutrient elements by the roots causing decline in plant growth (Tester and Davenport 2003; Maathuis 2014). With detrimental effect on germination, plant vigor, and crop yield, salinity is considered as one of the most severe factors checking the yield of agricultural crops (Munns and Tester 2008). Even at comparatively low salinity in soil, yield starts dropping in the larger part of cultivated plants (Chinnusamy et al. 2005). Hence, the management practice that is potent, cost-effective, and accomplished enough for increasing plant growth and productivity in soil-degraded areas is a challenge.

Where developing salt-tolerant germplasm has become difficult, however, the growth of various crops in salt-affected areas had been seen to embellish by some rhizospheric microorganisms. The exceptional quality of these rhizospheric microorganisms to tolerate the extreme conditions makes them a potent source to mitigate salt stress in crops grown in saline soils; their property to interact with plants as well as their distribution method helps for the commencement of a potential and promising approach for sustainable agriculture. Akhtar and Siddiqui (2010) define plant growth-promoting rhizobacteria (PGPR) to distinguish soil bacteria which after inoculation over seeds, pioneer the root system and promote the plant growth. These PGPRs contribute in the sustainable crop production by associating in numerous biotic activities of the soil community and make it essential for nutrient modification (Diby et al. 2005a, b; Akhtar and Siddiqui 2008, 2009). The PGPRs helps in triggering the growth of the plants by increasing the diverse production of plant growth regulators, mobilizing nutrient in soil, restricting and protecting from pathogens, bettering soil organization, and bioremediation of contaminated soil by separating various lethal heavy metals (Braud et al. 2009; Hayat et al. 2010). Studies done on PGPRs for proving its potentiality of maintaining productivity under stressed condition are now providing positive results. PGPRs are employed in the crop plants to defy stress caused by climate changes, thus contributing in understanding the stress tolerance, adaptation, and response procedure. (Grover et al. 2011). For the management of saline soil, soil biological activity must be boosted up so that they invigorate long-term soil productivity and crop health. Therefore, the aim of this chapter is to provide an overview of the soil-plant and microbial interactions in improving the salt stress condition.

10.2 Soil Salinity: The Magnitude of Problem

As soil salinization is speedily expanding in profuse part of the world, peculiarly in arid and semiarid areas, it has become a thoughtful problem (Giri et al. 2003; Al-Karaki 2006). Approximately 7% of the earth's agricultural area is affected by saline soil (Ruiz-Lozano et al. 2001), and by the mid of the twenty-first century, it has been estimated that farmable land will see a loss of about 50% land due to the increasing pace of soil salinization (Wang et al. 2003). Nearly 77 million ha of arable land, which contributes to about 5% of the cultivable land, is disrupted due to salinity (Sheng et al. 2008). According to Ruan et al. (2010), loss of about 12 billion USD is due to the salinity affecting nearly about 50% of the world's irrigated land (Flowers et al. 2010). Similarly, global loss of nearly about 27.3 billion USD has been estimated due to damage of crop production in salinity-affected arable areas (Qadir et al. 2014). The accurate estimation of agricultural loss which occurs in terms of decline in soil health and crop production by the abiotic stresses could not be formulated until now, but undoubtedly saline stress has affected a large part of cultivable land and influence both qualitative and quantitative losses in crop production (Cramer et al. 2011). In addition to the exploitation of accessible water resources, low rainfall, and high temperature in arid areas, increase in salinity of soil is also assisted by salts dissolved in irrigation water as well as in fertilizers (Cantrell and Linderman 2001; Al-Karaki 2006; Mouk and Ishii 2006). Soil salinity has massive consequences on the agricultural productivity (Tester and Davenport 2003) as it is the major reason behind the disruption in formation, growth, and advancement of plants, causing extensive damage to productivity (Giri et al. 2003; Mathur et al. 2007). Some of the consequences of salinity on plants are as follows:

(i) As a result of the decline in osmotic potential of the soil solution, plant-accessible water becomes reduced, leading to physiological drought, so to curb this situation, the inside osmotic potential of the plant must be controlled in order to avert water from coming back into the soil from the roots (Feng et al. 2002; Jahromi et al. 2008).
(ii) The disproportionate flux of Na^+ and Cl^- ions into the cells produces numerous harmful effects, including disruption in the structure of enzymes, damaged cell organelles and plasma membrane, and disturbance in various physiological functions (Juniper and Abbott 1993; Feng et al. 2002).
(iii) Improper transport of nutrient elements to the shoots causing ion deficiencies in the plants (Adiku et al. 2001).

10.3 Mitigation of Salt Stress in Crops by PGPRs

Microbes are the most important and essential part of the earth to regulate the influences of abiotic stresses and to increase the tolerance of crop plants toward these stresses. Through various studies, it was found that numerous microbial strains complement tolerance of plants to abiotic stresses like drought, salinity, nutrient deficiency or excess (Yang et al. 2008), and extreme load of heavy metals (Rajapaksha et al. 2004; Grover et al. 2011; Milošević et al. 2012). PGPRs amalgamate with the roots of the plants and alleviate most efficaciously the influence of abiotic stresses on plants by the genesis of exopolysaccharides and the formation of biofilm (Fig. 10.1). During stress conditions, rhizospheric microorganisms secure plants by employing various methods that alter plant cells like initiation of osmoprotectors and heat shock proteins. Microorganisms can be employed during the crop production for (i) checking soil's biological activity which includes microbial number and enzymatic activity, (ii) indicators of soil health, (iii) alleviation of destructive factors generated in plants by abiotic stresses, and (iv) beneficial and effective microorganisms as inoculants (Grover et al. 2011). Environmental factors influence the microbial association with soil in a large number. Some factors are mentioned as modulators like soil temperature, pH, salinity, and water potential (Balser et al. 2001), in contrast to the resources needed for the growth of microbial communities such as carbon and nitrogen. New and tolerant plant and microbial communities are evolving from the preceding one, in response to stress conditions,

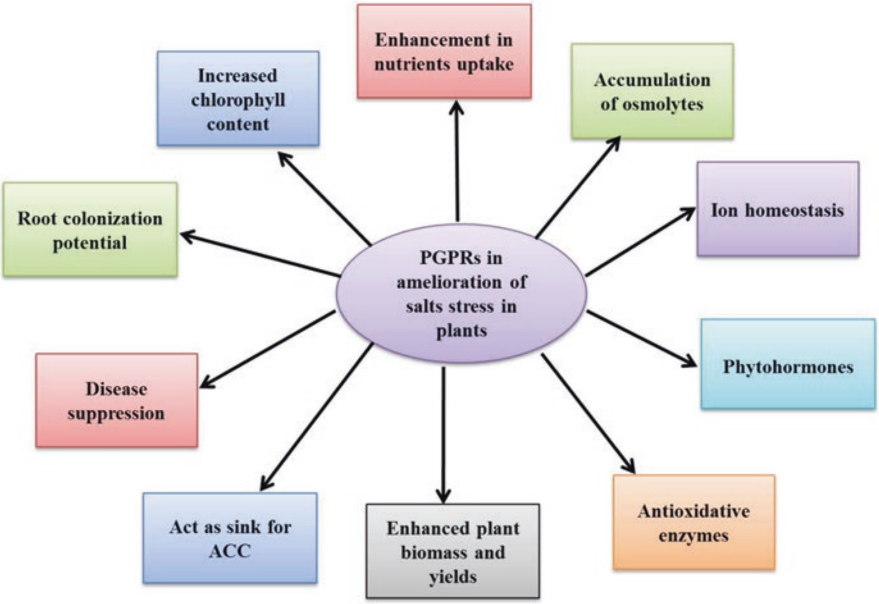

Fig. 10.1 Plant growth-promoting rhizobacteria colonize the rhizosphere of plants and promote growth of plants through various means and help mitigate salt stress

adapted through intricate regulatory means involving many genes (Milošević et al. 2012). A specific growth characteristic of bacterial species is exceptionally sensitive to environmental factors, and therefore it is a more dependable indicator of stress than metabolic activity (Bloem and Breure 2003; Rajapaksha et al. 2004). Growth and maturation of tomatoes, peppers, beans, and lettuce grown in saline habitat are affected by rhizobacterial strains (PGPR) (Grover et al. 2011; Yildirium and Taylor 2005). Wheat seedling inoculated with exopolysaccharide (EPS)-producing bacteria affects the regulation of sodium uptake and stimulation of plant growth under conditions of stress by high salinity (Ashraf 2004; Grover et al. 2011). When some crops like corn, beans, and clover were inoculated with arbuscular mycorrhizal (AM) fungi, the resistances toward salinity were increased as they augment their osmoregulation and elevate proline accumulation (Feng et al. 2002; Grover et al. 2011).

Intrinsic metabolic capabilities of the plant help often to manage the hasty variation and variety of environmental circumstances (Simontacchi et al. 2015). Microorganisms are valuable dwellers of soils as well as seeds, and there they proliferate with the seed development and form symbiotic association either on the surface or endophytically inside the root, stem, or leaves. The metabolic and genetic capacity of the microorganisms made them potent enough to resist acute circumstances of the environment (Sessitsch et al. 2012; Singh et al. 2014). Plants with symbiotic association with microorganisms have a better metabolic activity to combat abiotic stresses as these plants elicit numerous types of local and systemic responses (Nguyen et al. 2016). A testimonial of the important features of microbial interaction with plants helps in understanding the intensive mechanism of plant-microbe interactions that offer modulation of cellular, biochemical, and molecular mechanisms associated with stress tolerance (Bakker et al. 2012; Onaga and Wydra 2016). The study done at physiological, biochemical, and molecular level of plant-microbe interaction suggested that this association chiefly manages plant responses against stresses (Farrar et al. 2014).

10.3.1 How Do Salt Stresses Affect Plants

Numerous edaphic factors, chiefly alkalinity, salinity, acidity of soil (Bromham et al. 2013; Bui 2013), and anthropogenic activities (Emamverdian et al. 2015), adversely affect the plant growth and yield. Due to the acidity in soils, the available nutrients become restricted to the plants, because of which they become deprived of nutrients and hence lose their usual physiological functions (Rorison 1986). Salinity stresses can be managed by immediately fixing the osmotic and ionic equilibrium inside the cell. Plants follow various methods to fight salinity; they either distant their sensitive tissues from a region of excessive salinity or discharge ions from roots or may also separate ions from physiologically functional cell's cytoplasm (Silva-Sanchez et al. 2015). As soon as perceiving the stress stimulus, plants display an instantaneous and productive response by triggering intricate stress-specific signal cascade (Chinnusamy et al. 2004; Andreasson and Ellis 2010). This stress-specific signal cascade escalates the relevant defense mechanism by initiating the synthesis of phytohormone like abscisic acid, jasmonic acid, salicylic acid and ethylene (Spoel and Dong 2008; Qin et al. 2011; Todaka et al. 2012), flavonoids, and phenol accretion (Singh et al. 2011; Tiwari et al. 2011), augmentation of numerous antioxidants and osmolytes, and activation of transcription factors (Koussevitzky et al. 2008; Atkinson et al. 2013; Prasch and Sonnewald 2013). Regardless of having knowledge of stress tolerance mechanism in plants, the information about plant's on-field response to concurrent exposure to diverse stresses is still insufficient.

10.3.2 Soil Salinity: A Major Issue

Soil salinity is predicted as one of the severe problems affecting agricultural crop internationally in coming decades. According to Food and Agriculture Organization (FAO 2002), about 1–2% of the agricultural area is reduced every year because of soil salinization, striking vigorously in the arid and semiarid areas. Globally, due to the severe influence of soil salinity, it has been estimated that the productivity of roughly 400 million hectares of arable land is badly restricted (Bot et al. 2000). Approximately 6% of the earth's lands are affected by salt stress; of the 250 million ha of cultivable land, nearly 50% are under salt stress, and 10 million ha are converted into deserts every year as reported by the Food and Agriculture Organization of the United Nations, Land and Plant Nutrition Management Service (FAO 1988). Among abiotic hindrances, salt stress is acknowledged as the severe one as it not only affects the food production but also culminates into unfavorable economic, social, and ecological consequences. Salinity resulted in a loss in income by relatively 11 billion USD annually to the farmers, and the figure has kept on rising (Postel 1998). The numerous habitat forms of coastal wetlands and coastal agricultural zones were also affected by salt stress (Armstrong et al. 1985; Bharathkumar et al. 2008). In India out of the total of 8.1 million hectare saline lands, coastal region contributes nearly 3.1 million hectares of land (Tripathi et al. 2000).

10.3.3 Effect of Soil Salinity on the Growth and Development of Plants

Salinity influenced the growth and productivity of different crops in varying extent. Cereals, forages, and horticulture crops all are badly affected by salinity, which may be caused either through irrigated water or rhizospheric solution. Yields, nodulation, and the total nitrogen content in legume plants are said to be reduced because of salinity (Singleton and Bohlool 1984). The dry weight of various parts of the tomato plant was found to be reduced because of increment of NaCl level in the root growth medium (El-Fouly et al. 2001). Primary physiological functions of the plants, chiefly photosynthesis, protein synthesis, and lipid metabolism, all are majorly affected with the commencement and advancement of salt stress in the plant (Parida and Das 2005). Salinity is also responsible for membrane destabilization and nutrient imbalance in plants (Hasegawa et al. 2000). The increased amount of sodium, chiefly chloride, has the capability to affect plant enzymes and cause cell swelling; hence energy production and physiological changes are lowered (Larcher 1980). The photosynthetic activity of the plant is disturbed due to the uptake and accumulation of chloride ions which act as a barrier for nitrate reductase activity (Xu et al. 2000). Due to the high rhizospheric concentration of Na^+ and Cl^- ions, different other nutrients (K^+ and NO_3^- ion) also compete for binding sites and transport protein in root cells consequently for translocation, deposition, and partitioning within the plant (Tester and Davenport 2003). When the capacity of cell to accommodate salts becomes exhausted, the salts began to start accumulating in the intercellular spaces, causing cell dehydration and ultimately death (White and Broadley 2001).

Osmotic pressure in the root cells increases due to salinity, thus altering nutrient and water uptake. With increasing NaCl concentration in the growth medium, micro- and macronutrient contents decrease in the roots and shoots. The plants with disturbed nutrient relations are more sensitive to attack of different pathogenic microorganisms and physiological dysfunctions and conspicuously become less commercial, and their nutrient content declines because of shrunken fruit size and shelf life, irregular fruit shape, and drop in vitamin content (Romic et al. 2008). Salinity resulted into accumulation of reactive oxygen species, which are possibly destructive to biomembranes, proteins, nucleic acids, and enzymes (Porcel et al. 2012). Plant cells contain antioxidant and nonenzymatic antioxidants to safeguard against oxidative stress (Hasegawa et al. 2000), and the modulation of antioxidant enzyme activity and concentrations is often employed as an indicator of oxidative stress in plants (Mayak et al. 2004).

10.3.4 Effect of Soil Salinity on Microbial Diversity

The microorganisms form an important labile portion of the soil inorganic matter, having the capability to revolutionize and reprocess the organic content and soil nutrient and even act as a source of nutrients for the plants. Rhizospheric habitats of plants are more pleasant for microorganisms in comparison to the surrounding soil quantity (Bais et al. 2006), and directly or indirectly these microorganisms affect growth and development of plants. Moreover, as these microorganisms are handling the availability of nutrients to the plants, any element affecting their community and activities will ultimately affect the physiological processes of the plants. The activities of rhizospheric microbe population have several positive effects not only to the plant health in harmful environment but also as pollutant degradation in an ecosystem (Nie et al. 2009; Wenzel 2009). As the organic constituents of soil and microbial activity are usually more in the upper few centimeters of the soil surface, salinization close to this area can undoubtedly influence an array of microbiologically mediated functions. Salinity has an adverse effect on diversity and function of microbial community (Borneman et al. 1996). As reported by Omar et al. (1994), the entire amount of bacteria and actinobacteria was terribly decreased with an increase in the salinity level to above 5%. The destructive consequence of salt stress on the microbial soil communities and their functions is reported in naturally saline soils (Rietz and Haynes 2003; Sardinha et al. 2003). Moreover, high amount of salinity restricts nitrogen fixation at the level of nifH expression and nitrogenase activity in *Azospirillum* sp. (Tripathi et al. 2002). Root exudation and decomposition of organic matter by microorganisms are also severely affected due to salinity increase in the rhizosphere (Ondrasek et al. 2010). Li et al. (2006) also reported on the adverse effect of salinity on microbial biomass and activity by showing significant negative correlations between soil electrical conductivity and total CO_2 emission or microbial biomass carbon (C). As reported by Nelson and Mele (2007), rhizosphere microbial colony network is more likely to be affected by NaCl, indirectly through root discharge concentration than directly through microbial toxicity and that plant health is a significant determinant in rhizosphere microbial community structure. Bacterial growth is limited during salt stress, as the plant uses osmolytes making the rhizobacteria deprive of it. Different processes like protein alteration, change in polysaccharide content of bacteria, and restriction in movement of bacteria toward roots all are responsible for affecting microbial population in rhizosphere during saline environment. According to Ibekwe et al. (2010), alteration in microbial population may be considered as the first indicator of salt stress in soils. Consequently, if stress can be recognized early enough in saline soils, then some actions can be possibly performed to enhance the soil quality and crop productivity.

10.3.5 How to Manage Salinity Stress

Soil salinity is a strenuous task for farmers and agricultural scientists. Plant growth and microbial activity are severely influenced by the nutrient imbalance and accumulation of sodium and chloride ions in the soil. It has been investigated that the negative impact of salt on various plants can be checked by inoculation with plant growth-promoting (PGP) microbes and endophytic microbes (Table 10.1). Under saline environment, various damaging effects can be mitigated by biofilm formed by PGP microbes (Kasim et al. 2016). Salt-tolerant bacteria co-inoculated with arbuscular mycorrhizal (AM) fungi significantly boost the salinity tolerance in some plants. In maize plant, the co-inoculation of *Rhizophagus intraradices* and *Massilia* sp. RK4 invigorates arbuscular mycorrhizal fungi (AMF) root colonization and nutrient accumulation under salt stress (Krishnamoorthy et al. 2016).

10.4 Mechanism of Salinity Stress Tolerance

Ability of microbes to tolerate salinity stress helps plants in improving growth under stress environment. Two types of mechanisms are mainly involved, namely, direct or indirect (Fig. 10.2). Production of phytohormones, viz., auxin, cytokinin, ethylene, and gibberellins, nitrogen fixation, nutrient flow, and formation of siderophore

Table 10.1 Summary of PGPR interaction effects in crop plants under salinity stress from recent studies using systems biology approaches

Plant	Microbe	Effect/mechanism	References
Abelmoschus esculentus	*Enterobacter* sp. *UPMR18*	Increase antioxidant enzyme activities and upregulation of ROS pathway genes	Habib et al. (2016)
Arabidopsis thaliana	*Bacillus subtilis*	Tissue-specific regulation of sodium transporter HKT1	Zhang et al. (2008)
Arabidopsis thaliana	*Pseudomonas syringae DC3000*, *Bacillus* sp. strain *L81*, *Arthrobacter oxidans*	SA-dependent pathway	Barriuso et al. (2008)
Arachis hypogea	*Brachybacterium saurashtrense*	Higher K^+/Na^+ ratio and higher Ca^{2+}, phosphorus, and nitrogen content. Shoot and root has higher concentration of auxin	Shukla et al. (2012)
Arachis hypogea	*P. fluorescens*	Enhanced ACC deaminase activity	Saravanakumar and Samiyappan (2007)
Brassica napus and *Zea mays*	*P. putida*	Modulation of plant protein differential expression and ACC deaminase activity	Cheng et al. (2011)
Capsicum annuum	*Azospirillum brasilense* and *Pantoea dispersa*	High stomatal conductance and photosynthesis	del Amor and Cuadra-Crespo (2012)
Glycine max	*Bacillus thuringiensis NEB17*	Upregulation of PEP carboxylase, RuBisCO oxygenase large subunit, pyruvate kinase, and proteins of photosystems I and II, isocitrate lyase, and antioxidant glutathione-S-transferase	Subramanian et al. (2016)
Glycine max	*Pseudomonas simiae*	Upregulation of vegetative storage proteins, RuBisCO large chain proteins. Decrease in root NaCl accumulation and increase in proline and chlorophyll content	Vaishnav et al. (2015)
Glycine max	*Glomus etunicatum*	Increased root but decreased shoot proline concentrations	Sharifi et al. (2007)
Glycine max	*Glomus intraradices*	Accumulation of carbohydrates	Porcel and Ruiz-Lozano (2004)
Gossypium hirsutum	*P. putida Rs-198*	Increase the absorption of the Mg^{2+}, K^+, and Ca^{2+} and decrease the uptake of the Na^+ from the soil	Yao et al. (2010)
Gossypium hirsutum	*Raoultella planticola Rs-2*	ACC deaminase activity	Wu et al. (2012)

(continued)

Table 10.1 (continued)

Plant	Microbe	Effect/mechanism	References
Hordeum vulgare	*Hartmannibacter diazotrophicus*	Increased root and shoot dry weight. ACC deaminase activity and lower ethylene content	Suarez et al. (2015)
Hordeum vulgare and *Avena sativa*	*Acinetobacter* spp. and *Pseudomonas* sp.	Production of enzyme ACC deaminase, lower ethylene, and IAA promote plant growth	Chang et al. (2014)
Lactuca sativa	*G. intraradices BEG121*	Reduced concentration of ABA	Aroca et al. (2008)
Lactuca sativa	*B. subtilis*	Root-to-shoot cytokinin signaling and stimulation of shoot biomass	Arkhipova et al. (2007)
Lactuca sativa cv. Tafalla	*P. mendocina*	ACC deaminase activity and enhanced uptake of essential nutrients	Kohler et al. (2009)
Lactuca sativa	*Azospirillum* sp.	Promoted higher biomass, ascorbic acid content antioxidant capacity, and a lower browning intensity	Fasciglione et al. (2015)
Lotus glaber	*G. intraradices BAFC 3108*	Decreased root and shoot NaCl accumulation and enhanced root KCl concentrations	Sannazzaro et al. (2006)
Lycopersicon esculentum	*Achromobacter piechaudii*	Reduced levels of ethylene and improved plant growth	Mayak et al. (2004)
Oryza sativa	*B. amyloliquefaciens*	Modulating differential transcription in a set of at least 14 genes	Nautiyal et al. (2013)
Oryza sativa	*P. pseudoalcaligenes*, *B. pumilus*	Increased concentration of glycine betaine	Jha et al. (2011)
Oryza sativa GJ-17	*P. pseudoalcaligenes* and *B. pumilus*	Reduced the toxicity of reactive oxygen species (ROS) and reduce lipid peroxidation and superoxide dismutase activity. Reduce lipid peroxidation and superoxide dismutase activity	Jha and Subramanian (2014)
Phaseolus vulgaris	*Azospirillum brasilense strain Cd*	Stimulation of persistent exudation of flavonoids	Dardanelli et al. (2008)
Phragmites australis	*G. fasciculatum*	Accumulation of carbohydrates	Al-Garni (2006)
Solanum lycopersicum	*P. putida UW4*	Increased shoot growth and expression of Toc GTPase	Yan et al. (2014)
Solanum lycopersicum “Micro tom”	*Streptomyces* sp. *strain PGPA39*	ACC deaminase activity and IAA production and phosphate solubilization	Palaniyandi et al. (2014)

(continued)

Table 10.1 (continued)

Plant	Microbe	Effect/mechanism	References
Triticum aestivum	*Aeromonas hydrophila/caviae*, *B. insolitus*, *Bacillus* sp.	Exopolysaccharide production	Ashraf (2004)
Triticum aestivum	*P. putida, E. cloacae*, *Serratia ficaria*, and *P. fluorescens*	Enhanced germination percentage, germination rate, and index and improved the nutrient status of the wheat plants	Nadeem et al. (2013)
Triticum aestivum	*Triticum aestivum*	Modulation of ABA signaling cascade, SOS pathway-related genes, tissue-specific responses of ion transporters	Bharti et al. (2016)
Vigna radiata	*PGPR* (*Mk1*, *Pseudomonas syringae*; *Mk20*, *Pseudomonas fluorescens*; *and Mk25*, *Pseudomonas fluorescens biotype G*) and *Rhizobium phaseoli strains M1*, *M6*, and *M9*	ACC deaminase activity and improvement in growth and nodulation in mung bean	Ahmad et al. (2011)
Vigna radiata	*Rhizobium phaseoli* and *PGPR* (*Pseudomonas syringae*, *Mk1*;*Pseudomonas fluorescens*, *Mk20*; and *Pseudomonas fluorescens Biotype G*, *Mk25*)	ACC deaminase activity and increased water use efficiency	Ahmad et al. (2012)
Zea mays	*Pseudomonas* and *Enterobacter*	Reduce triple response and more N, P, and K uptake and high K^+–Na^+ ratios	Nadeem et al. (2009)
Zea mays	*Azospirillum*	Restricted Na^+ uptake and increased K^+ and Ca^{2+} uptake along with increased nitrate reductase and nitrogenase activity	Hamdia et al. (2004)
Zea mays	*Rhizobium* sp., *Pseudomonas* sp.	Decreased electrolyte leakage and increase in proline production, maintenance of relative water content of leaves, and selective uptake of K ion	Bano and Fatima (2009)
Zea mays	*B. amyloliquefaciens SQR9*	Upregulation of RBCS, RBCL, HKT1, NHX1, NHX2, and NHX3	Chen et al. (2016)
Zea mays	*B. megaterium*	Improved expression of two ZmPIP isoforms	Marulanda et al. (2010)

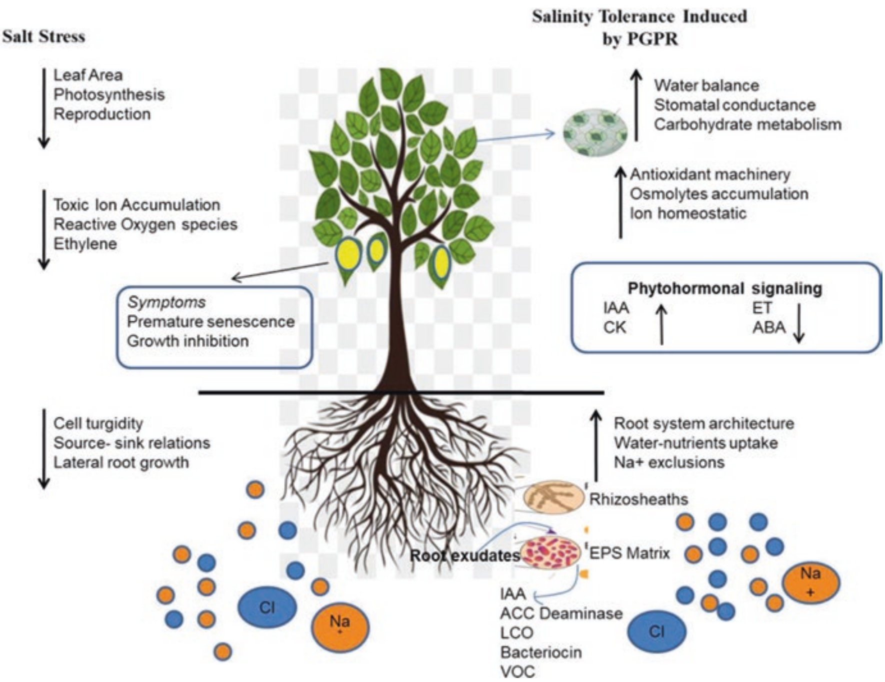

Fig. 10.2 Illustration of salt tolerance mechanisms induced by plant growth-promoting rhizobacteria

all fall in the category of direct mechanisms (Hayat et al. 2010). These include various types of mechanisms and mode of reactions and bring about an enhancement in root length, leaf surface area, and number of roots resulting in mineral absorption (Egamberdieva and Kucharova 2009). Decline in the intensity of pathogen-induced diseases in flora is the main aim of indirect mechanism. An enzyme 1-aminocyclopropane-1-carboxylate deaminase (ACCD) produced by rhizobacteria plays a role in the conversion of ACC into nitrogen-containing compounds, ammonia, and α-ketobutyrate and decreases ethylene level. Under stress environment, microbial extracellular polymeric substance (EPS) provides resistance against salinity by binding with cations and hence makes it unavailable to plants (Vardharajula et al. 2010). Features of plant growth-promoting rhizobacteria, viz., formulation of indole-3-acidic acid, ammonia, and hydrogen cyanide, mobilization of phosphate, and capacity of salt tolerance, were also shown by some species of *Bacillus* sp. (Damodaran et al. 2013). Salinity tolerance was increased in rice plants when inoculated with *Pseudomonas* sp. and *Bacillus* sp. and exhibits elevated amount of glycine betaine (GB) (Jha et al. 2011). During salt stress, *Acinetobacter* spp. and *Pseudomonas* spp. promote plant growth in barley and oats by producing ACC deaminase and IAA (Chang et al. 2014). Species of *Azospirillum* improve the morphological parameters and yield of wheat under water salinity condition (Nia et al. 2012). In maize, a phytohormone like abscisic acid plays an important job in saline condition by acidification of apoplast. Lettuce seed treated with *Azospirillum* sp. increases growth of lettuce plant, purity of product, and life under stress environment (Fasciglione et al. 2015). A plant growth-promoting rhizobacteria, viz., *Hartmannibacter diazotrophicus* E19 separate from *Plantago winteri*, under saline conditions improve plant growth of barley (Suarez et al. 2015). Three PGPRs extracted from some bacterial spp., viz., *Pseudomonas*, *Bacillus*, and *Mycobacterium*, have the capacity to sustain in saline soil, i.e., calcisol soil (Egamberdiyeva 2007). In *Zea mays*, co-inoculation of plant growth-promoting rhizobacteria, *Rhizobium* and *Pseudomonas*, improves salt tolerance by increasing build-up of proline content with lessened electrolyte leakage and preservation of relative water content of leaves and by selective absorption of potassium (Bano and Fatima 2009). Some species of *Pseudomonas* spp. obtained from the root zone of tomato plant have the potential to produce plant growth hormones and 1-aminocyclopropane-1-carboxylate deaminase (ACCD) enzyme which helps to increase the salt tolerance power of tomatoes (Bal et al. 2013; Tank and Saraf 2010). Shahzad et al. (2017) found that plant growth hormones, viz., abscisic acid and auxin, obtained from *Bacillus amyloliquefaciens* sp. have the capability to promote tolerance to salt stress in rice. Involvement of tricarboxylic acid cycle in tomato plant acts as a barrier against salt stress conditions (Torre-González et al. 2017).

10.5 Conclusions and Future Prospects

Microorganisms lie in close association with the plant and play an important role against salt stress resistance via numerous types of mechanisms, viz., regulating osmotic response and incorporation of peculiar genes in plants. The process of development of salt stress-tolerant crop cultivar by biotechnological approach and plant breeding is an effective technique; on the other hand it is a time-consuming and tedious job. However, incorporation of microorganisms will mitigate salt stress in plants, and the most important thing is that it is a cost-effective and eco-friendly approach and is a feasible option. Taking the current leads, an advance research is needed in the future in this area, mainly field assessment and application of able microorganisms.

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11

Plants Growing Under Salinity Stress Can Be Eased Through Mycorrhizal Association

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Abstract

Environmental stresses like drought, extreme cold or heat, high wind, pH, salt, toxic compound, and infection by insects or parasites are largely affecting living organisms on earth. Soil salinity is one of the world's major environmental problems in agriculture. The major cause of salinity is through natural process or human-induced progressions, resulting in the accumulation of dissolved salts in the soil water which affects plant growth. Therefore soil salinity coupled with land deprivation is the most alarming ecological problem. Salinity reduces the net photosynthetic rate, stomatal conductance, and relative water content, and these dreading effects can be diluted by mycorrhizal association. Among the biological strategies to improve plant growth under saline conditions, the most credited and valued role comes from arbuscular mycorrhizal (AM) fungi. Arbuscular mycorrhiza is a symbiotic relationship between fungi and plants and plays a pivotal role in nutrient cycling and stress tolerance. Under saline conditions, mycorrhizal association significantly relieves the salt stress by improving physio-biochemical features that could be primarily attributed to net increase in photosynthetic efficiency, enhanced nutrient acquisition, root hydraulic conductivity, and stabilization of osmotic balance. Therefore, the aim of this chapter is to explore the mechanism by which mycorrhiza is making plant less stressed under saline conditions.

Keywords

Arbuscular mycorrhiza · Environmental problem · Nutrient acquisition · Salt · Salinity

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11.1 Introduction

Soil salinity is a major limiting factor in production and productivity of agricultural crop mainly in arid and semiarid regions having high evaporation and low precipitation rate (Nachshon 2018). High content of soluble salt may interfere with germination of seed, growth and development, and yield of the plant and thus can transform a fertile land into a barren land (Munns and Tester 2008). According to the FAO Land and Plant Nutrition Management Service, more than 7% of the world's agricultural land is affected by either salinity or sodicity. Worldwide, salinity caused demolition of more than 45 million ha of irrigated land, and every year 1.5 million ha of irrigated land lost their productivity as a result of high salinity levels in the soil (Munns and Tester 2008). Nachshon (2018) reviewed that roughly 20% of total cropland and 33% of irrigated agricultural land are salinized, and it is expected that by 2050, it may affect half of the croplands worldwide. Natural phenomenon or human-induced progressions result in the accumulation of dissolved salts in the soil water which may affect plant growth. Sodicity is a secondary effect of salinity in clay soils, where leaching may lead to washing of soluble salts into the subsoil, and left sodium bound to the negative charges of the clay.

There are numerous effects of salinity on the plant, including water stress, ion toxicity, nutritional disorders, oxidative stress, alteration of metabolic processes, membrane disorganization, genotoxicity, and reduction of cell division and expansion, which ultimately reduce plant growth, development, and survival (Hasegawa et al. 2000; Munns 2002; Zhu 2007). Initially, salt stress within a plant affects all the major processes such as photosynthesis, protein synthesis, and energy and lipid metabolism (Parida and Das 2005). If prolonged, it reduces leaf expansion, resulting from inhibited cell expansion and cell division, as well as stomatal closure (Munns 2002; Flowers 2004). The long-term exposure to salinity also causes ionic stress in the plant, which may lead to premature senescence of adult leaves due to chlorosis and necrosis in mature leaves, and thus reduction in the photosynthetic area of the plant (Cramer and Nowak 1992). High concentration of Na^+ may interfere in protein synthesis and enzyme activity (Munns and Termaat 1986; Munns 2002). A fundamental biological understanding and knowledge of the effects of salt stress on plants is necessary to provide additional information for the understanding of the plant response to salinity and mycorrhiza in improving the performance of species important to human health and agricultural sustainability. Therefore, the aim of this chapter is to explore the mechanism by which mycorrhiza is making plant less stressed under saline conditions.

11.2 Types and Causes of Salinity

Salinity is the presence of high concentration of dissolved mineral salts in soils (soil solution) and waters to the extent required for the suitable growth of plant. The dissolved mineral salts consist of electrolytes of cations and anions. The main cations present in saline soil solutions are Ca^{2+}, Mg^{2+}, Na^+, and K+ and the anions as SO_4^{2-},

HCO_3^-, Cl^-, NO_3^-, and CO_3^{2-}. Hypersalinity in the soil may be due to B, Mo, Sr^{2+}, SiO_2^+, Ba^{2+}, and Al^{3+} (Hu and Schmidhalter 2002). Salts get accrued in the upper part of the soil profile, including the A and B horizons or mantle of fragmental and unconsolidated rock material which impacts on agricultural production, environmental health, and economic welfare (Rengasamy 2006). The principal source of salt is rainfall and rock weathering.

11.3 Impacts of Salinity

The detrimental impacts of salinity decrease agricultural production of crop plants affecting the economic returns because of high cost of cultivation. Soil salinity also has an impact on physicochemical properties and ecological balance of that area (Hu and Schmidhalter 2002). Saline soil enforces toxic effect of ions, osmotic stress and paucity of nutrients that result in physiological stress on plants leading to limited water absorption from soil. Besides, it greatly decreases uptake of phosphorus because phosphate ions precipitate with Ca ions (Shrivastava and Kumar 2015). Ecological imbalance in halophytes and marine life forms from fresh water to brackish water and toxic effects of elements such as B, F, and Se may lead to severe human diseases

The effects of a saline soil are twofold: effects of the salt outside the roots and effects taken up by plants. Salt stress leading to conditions like water deficit (drought stress), ion toxicity, ionic imbalance, and soil compaction may cause growth reduction, injury of foliage, nutrient deficiencies, and demolition of soil structure which ultimately hampers the growth of the plant. The morphological symptoms of plants are marginal yellowing/browning of foliage, premature falling of leaves, twig and branch dieback, loss of vigor, and stunted growth. Further, salt stress also may inhibit the uptake of important mineral nutrients, such as K^+ and Ca^{2+}, which further reduces root cell growth (Larcher 1980). Under salt stress, there are increase in concentration of Na^+ and Cl^- and reduction in K^+ and Ca^+ content which cause major problems like increase in osmotic stress and decrease in water potential. Due to salinity germination, development, photosynthesis, protein synthesis, lipid metabolism, leaf chlorosis, senescence, etc. (Muthulakshmi et al. 2013) are damaged. Moreover, salt stress had been found responsible for increased respiration rate and ion toxicity (Sudhir and Murthy 2004), decreased biosynthesis of chlorophyll (Khan et al. 2009), and inefficiency of photosynthesis (Munns 2002). Several metabolic alterations in response to water deficit can occur in plant tissue at one of the following three levels: (i) disturbance of metabolic pathways leading to an accumulation or loss of metabolites; (ii) alterations in enzyme activities; and (iii) changes in the patterns of protein synthesis (Khalil and Yousef 2014). Salt treatment decreases root and shoot weight and chlorophyll content in salt-sensitive genotypes more than salt-tolerant genotypes. Salinity stress reduces photosynthetic activity which results in decrease in chlorophyll b and a. (Nazarbeygi et al. 2011).

At low salt concentrations, yields of agricultural crops are insignificantly affected or not affected at all (Maggio et al. 2001). As the concentration increases, the yield of the crop reduced to zero. Most plants, glycophytes, including most crop plants do not grow in high concentrations of salt and are severely inhibited or even killed by 100–200 mM NaCl. The reason is that they have evolved under conditions of low soil salinity and do not display salt tolerance (Munns and Termaat 1986). Medicinal plants are rich in secondary metabolites like alkaloids, glycosides, steroids, and flavonoids. Biosynthesis of secondary metabolites is strongly affected by salt stress resulting in considerable fluctuations in their quality and quantity (Turkmen et al. 2005).

11.4 Biochemical Changes

Under saline stress, water potential of soil gets more negative due to less water, restricting the movement of water to roots. Therefore, to combat this problem, plants decrease their water potential through mainly osmoregulation by vigorous augment of organic ions or solutes (Morgan 1984; Hoekstra et al. 2001). Plants grown under salt stress accumulate nitrogenous compounds like amino acids, polyamines, and betaines (Rabie and Almadini 2005). Osmotic adjustment permits the cellular expansion and growth, stomatal opening, and photosynthesis while maintaining turgor pressure favorable to water absorption by the plant. Evelin et al. (2009) reported proline to be one of the main accumulates able to restore the water potential under salt and draught stress. Plants colonized with AMF accumulate more proline and are reported to have better adaptation under stress. On the contrary there are reports (Rabie and Almadini 2005) where accumulation of proline is due to salinity and not essentially by mycorrhizal colonization as reported by Sannazzaro et al. (2006). Free polyamines generally decrease under saline conditions, but in association with AMF, it increases (Sannazzaro et al. 2007). During salt stress plants reduce the osmotic potential by accumulating soluble sugars (Thanna and Nawar 1994) which increases further on inoculation with mycorrhiza (Thomson et al. 1990; Al-Garni 2006). This constructive relationship between sugar content and AMF colonization is due to the sink effect of the mycorrhiza challenging sugars from the host plant (Auge 2000). Mycorrhization increases the photosynthetic rate (Finlay and Soderstrom 1992) and may also be due to hydrolysis of starch to sugars in the seedlings inoculated with mycorrhiza (Nemec 1981). Salt stress manipulates various physiological processes like nutrient uptake, photosynthesis, respiration, protein synthesis, lipid metabolism, and water absorption in plants (Marschner 1995; Adiku et al. 2001; Ramoliya et al. 2004), thus leading to poor growth of plants.

11.5 Mycorrhiza and Salt Stress

In nature, plants associated with several microorganisms, such as bacteria and fungi, help in sustaining them during various environmental pressures. Mycorrhizal fungi have been reported on the roots of cultivated and non-cultivated plants found in disturbed or undisturbed saline soil. Evelin et al. (2009) reported that sporulation in mycorrhiza enhances in soil with large amount of salt in it, and it is particularly of *Glomus intraradices*, *G. versiform*, and *G. etunicatum.* Shekoofeh and Sepideh (2011) observed that under saline conditions, mycorrhizal inoculated plants experienced increase in root length, dry and fresh weights of shoot, and content of photosynthetic. These have been associated with increased plant biomass and growth in saline soil (Ruiz-lozano and Azcon 2000). Studies in plants such as tomato (Al-Karaki 2006) and soybean (Sharifi et al. 2007) showed increased growth under saline conditions during their roots colonization by AM fungi. It has been reported by many researchers that AMF-inoculated plants developed more efficiently than non-inoculated plants under salt stress (Al-Karaki 2000; Cantrell and Linderman 2001; Giri et al. 2003; Sannazzaro et al. 2007; Zuccarini and Okurowska 2008). AM fungi have been shown to promote plant growth and salinity tolerance by utilizing various mechanisms, such as (A) enhancing nutrient uptake (Evelin et al. 2013); (B) producing plant growth hormones; (C) improving rhizospheric soil conditions (Asghari et al. 2005); (D) improving photosynthetic activity or water absorbing efficiency (Hajiboland et al. 2010); (E) accumulating compatible solutes (Evelin et al. 2013); and (F) producing higher antioxidant enzymes (Manchanda and Garg 2011). These beneficial alterations make AM fungi suitable for bio-amelioration of saline soils.

The incongruities in various studies proposed that various AM fungal spp. have varying tolerance to salinity, depending upon the host plant and AM fungus compatibility and tolerance (Porras-Soriano et al. 2009). Interacting factors affecting the successful combination of vesicular arbuscular mycorrhiza (VAM) fungi are pH, soil nutrients, organic matter, moisture, and temperature. *G. mosseae* favors neutral to alkaline pH for germination, while spores of *Gigaspora* germinated best between pH 5 and 6. Hepper (1984) determined the optimum range required for the germination of *Acaulospora laevis* in soils as 4–5. Juniper and Abbott (1993) and Carvalho et al. (2001) reported the development of arbuscular mycorrhizal fungi from spore germination to root colonization is generally inversely proportional to salt concentrations and thus concluded that the distribution and development of mycorrhizas in salt marsh are more dependent on host plant species than on environmental stresses. Salinity induces a significant decrease in the contents of pigment fractions in both chlorophyll a and b and was found directly correlated with the concentration of salt. Mycorrhizal and saline condition had strong effects on leaf chlorophyll content. A reduction in the content of plant chlorophyll with an increase in the concentration of salt in the soil is attributed either to suppression of specific enzymes involved in the biosynthesis of photosynthetic pigments (Sheng et al. 2008) or due to increase in the activity of chlorophyll-degrading enzyme, chlorophyllase (Jamil et al. 2007). In fact, salt stress opens porphyrin rings resulting in transfer of harmful substances to vacuole. Presence of these compositions demolishes the green color of leaf and ultimately reduces the chlorophyll concentration of the leaf (Parida and Das 2005). Ramakrishnan and Bhuvaneswari (2015) clearly indicated the antagonistic effect of NaCl on N absorption, an essential component of the structure of chlorophyll molecule. They also reported that soil salinity markedly reduced the chlorophyll content in non-mycorrhizal plant leaves with chlorosis but not observed in plants colonized by AMF. A reduction in the uptake of minerals (e.g. Mg) needed for chlorophyll biosynthesis also reduces in the leaf (Desouky and Atawia 1998). However, presence of mycorrhiza significantly controlled the reduction of chlorophyll a and b content under saline condition and maintains the overall growth of plant. It means mycorrhiza helps in combating the salt stress in plants. Similar reports by Giri and Mukerji (2004), Sannazzaro et al. (2006), Sheng et al. (2008), Abdelgawad et al. (2014), Hassan and Ali (2014), and Zuccarini (2007) support the effect of mycorrhiza in mitigating saline stress. This concludes that interference of salt with chlorophyll synthesis gets reduced in plants associated with mycorrhiza than in non-mycorrhizal plants. In the presence of mycorrhiza, the antagonistic effect of Na^+ on Mg^{2+} uptake is counter balanced and suppressed (Giri and Mukerji 2004). Zhu et al. (2010) showed an increase in photosynthesis rate, transpiration, and chlorophyll a and b content under cold stress in maize plant inoculated with *G. etunicatum*. These findings are also in accordance with these findings and strongly support that mycorrhizal under saline condition had strong recovery effects on leaf chlorophyll content. The soil salinity drastically lowered leaf chlorophyll a and b content of non-mycorrhizal plants, but with mycorrhizal inoculation, it lowered the effect of stress considerably.

In salt stressed plants, synthesis and accumulation of proline is a primary defense response required in adjusting osmotic pressure (Beltrano et al. 2013). However, there are reports showing reduction in proline levels in AM plants under salt stress (Jahromi et al. 2008). Increase in proline accumulation was reported as an adaptive response to salinity in different plants such as sugar beet (Farkhondeh et al. 2012) and tobacco (Celik and Atak 2012). Alqarawi et al. (2014) found that there was increase in content of proline, phenol, and lipid peroxidation with increasing concentration of NaCl, but lower accumulation has been reported in plants treated with AMF. This increase in proline could be due to the induction of proline biosynthesis enzymes and/or the reduction of oxidation to glutamate (Stewart 1981). Proline has a key role in scavenging reactive oxygen species (ROS) (Miller et al., 2009), osmotic adjustment (Sheng et al. 2011), and facilitating water uptake (Hassine and Lutts 2010). The accumulation of proline in plants and its role in osmotic adjustment are well established. Proline accumulation helps in maintaining cell metabolism during scarcity of water, thus enabling plant survival under extremely severe conditions. The capacity of the plant to accumulate proline under saline conditions is positively correlated with salt concentration in the irrigation water. The level of free proline in Ashwagandha plants measured after 8 days revealed that under nonstress conditions, the level of proline was low and it steadily increased with the supply of salt to the soil (Parihar and Bora 2018). The reduced amount of proline in AMF plants gives a clear indication that these plants were less stressed, as compared to plants without mycorrhiza. Synthesis of proline in plants is through two pathways: glutamate and ornithine. The main production of proline is through glutamate under osmotic stress. Celik and Atak (2012) reported that during osmolite accumulation, proline oxidase is the main regulatory enzyme which converts proline into glutamate. Further, they reported that accumulation of proline with stress tolerance is having a negative correlation. In the present study too, plant with mycorrhiza has more stress tolerance but reduced proline content as compared to control.

Salinity in the soil greatly disturbs the availability, competitive uptake, and translocation of nutrients to different parts of the plant. The major factor which increases salinity in the fertilized land is the use of saline water for irrigation and application of fertilizer (Epstein et al. 1980). High salt concentration in the plant tissues can bring change in morphological, physiological, and metabolic processes of the plants via two mechanisms: osmotic and ionic stresses (Hasegawa et al. 2000). High amount of Na^+ and Cl^- ions in plants shows deleterious effect on cell membrane functions. Salinity stress in plant triggered by excessive uptake of sodium chloride ions from the soil plant which causes reduction in water gradient between root and soil solution finally results into osmotic stress condition. Ion accumulation decreases water gradient between root and soil solution, making it more difficult for water to move through the root surface (Flowers and Yeo 1986). Further extreme deposition of ions, mainly Na^+, which is a non-essential element (except in some C_4 plants) in the plant tissues results in alteration of physiological and biochemical processes (Munns 2005; Nieves-Cordones et al. 2016), and its excess accumulation will be highly deleterious to the plants.

The excessive amount of salt results in induction of cytosolic K^+ efflux and consequently an imbalance in cellular homeostasis, oxidative stress, interference with Ca^{2+} and K^+ functions, nutrient deficiency, retarded growth, and even the death of plant cells (Tester and Davenport 2003; Munns and Tester 2008; Craig Plett and Møller 2010; Cabot et al. 2014). Water absorption capacity of plants is improved by rising root hydraulic conductivity, maintaining osmolarity and carbohydrates level (Evelin et al. 2009). Juniper and Abbott (1993) opine that it could be increasing the plant growth and temper the hazardous effect of ions. Farooq et al. (2017) reviewed the effect of salt stress and found 50% decline in seed germination due to impeding of water uptake from the root and the deleterious effect of excessive salt to the embryo. Further it resulted in more than 70% drop in growth, uptake in minerals and nutrients, and finally shortening in the yield of plant which varied from 12% to 100% due to reduced photosynthesis, imbalance in hormonal regulation, and accumulation of toxic ions. Hasan and Miyake (2017) found anatomical damage of roots and leaves of maize plants after 2% and 3% NaCl treatment. They also observed shrinkage of epidermis cells and parenchyma cells of cortex and pith and epidermal and mesophyll cell of the leaf using scanning electron microscope (SEM). Further it results in alteration of nutrient uptake like the contents of aluminum, calcium, iron, magnesium, sodium, and chlorine which were found higher, while boron, potassium, and phosphor were lower in NaCl-treated plants as compared to control one.

Arbuscular mycorrhizal (AM) fungi act as growth regulator for the host plant and alleviate the harmful effects of salt stress. Presence of mycorrhiza normalizes K^+/Na^+ ratios in plant tissues; osmotic balance by accumulation of proline, glycine betaine, or soluble sugars; and supply of essential nutrients from the soil to the host plan, thus stabilizing the uptake mechanism in plants. Therefore, the plant recuperates the water balance machinery, enhancing their tolerance capacity and thereby enduring the salt stress (Porcel et al. 2012).

Selvakumar et al. (2014) reviewed arbuscular mycorrhizal fungi extensively found in salt-stressed region. AMF enter the cortical cells of plant root and form arbuscules which are exploited as nutrient exchange sites. Besides, it forms vesicles in between the cortical cells to store nutrients. During salt stress condition, AMF spread out their extra radical hyphae into non-rhizosphere soil to increase the uptake of nutrients and make it available to the plant. Krishna et al. (2018) detected that association of chili plants with mycorrhiza alleviated drought condition and revealed tolerance under stress among control cultivars. They found increase in the root biomass which proposed that colonization of chili with mycorrhiza has reduced the water stress by increasing water and nutrient exchange between soil and roots of host plant. Further, there was decrease in cellular damage by maintaining cell membrane integrity. Hence, inoculation of AMF to hot pepper cultivars ought to be considered as one of the most efficient methods for enhancement of drought tolerance, thereby achieving sustainability in agriculture.

11.6 Conclusions and Future Prospects

Association of AMF not only endorses plant growth but also enables the plant to fight for salinity tolerance through a range of mechanisms such as increasing absorption of nutrients, stimulating phytohormone production, adjusting the host's physiology, and shielding roots against soilborne pathogens. The present chapter deals with the deleterious effect of soil salinity in diverse areas of agricultural crops ultimately upsetting our agro-economy. Soil salinity reduces the crop yield and imposes osmotic stress on plants, but these issues could be resolved to a large extent by mycorrhizal association. Thus, in future, more researches are desired on mycorrhizal fungi to explore it as an effective bio-gizmo in mitigating the salinity stress.

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12 Halophilic Microbe Interactions with Plants to Mitigate Salt Stress

Sanjay Arora and Divya Sahni

Abstract

Because salt-affected soils including saline, sodic, and saline-sodic soils, are poor in organic matter content, biomass and microbial activity are significantly affected, thereby affecting the microbiologically mediated processes required for plant growth. Halophilic microbes are those that are present in saline environments. During the recent past, the diversity and ecology of halophiles have been studied by several workers. In salt-affected soils, several species of halophiles have been isolated and reported from different parts of the world. Endophytes from halophilic plants have also been isolated and reported from hypersaline areas. Halophiles have a mechanism to tolerate salt stress by expressing aminocyclopropane-1-carboxylic acid (ACC) deaminase activity that removes stress and ethylene from the rhizosphere, and some halophiles produce auxins that promote root growth. Plant growth-promoting (PGP) bacteria that thrive in association with roots of the plants alleviate salt stress for improved plant growth and yield through their own mechanisms of osmotolerance, osmolyte accumulation, nonsymbiotic nitrogen fixation, solubilization and mineralization of essential plant nutrients, and production of useful plant hormones. Plant growth-promoting bacteria induced salt stress tolerance in plants has been studied to come up with a cost-effective solution for saline soils and improve agricultural crop yields. Salt-tolerant arbuscular mycorrhizal fungi (AMF) is also known to mitigate soil salinity stress and improve agricultural crop on inoculation in salt-affected soils. Inoculation of halophilic plant growth-promoting bacterial strains mitigates salt stress and enhances crop growth and yields. Thus, the aim of the present chapter is to focus on halophilic microbe interactions with plants to mitigate salt stresses.

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Halophiles · Arbuscular mycorrhizal fungi · PGPR · Salt tolerance · Hypersaline environment · Bioremediation · Salt-affected soil

12.1 Introduction

Globally the salt-affected area covers an area ranging from 340 million ha to 1.2 billion ha (FAO 2008). The salt-affected area is gradually expanding due to improper soil and water management and waterlogging and soil salinization resulting from the introduction of irrigation in arid, semiarid, and subhumid regions. Rise in the water table is inevitable upon introduction of irrigation network without provision for adequate drainage. According to FAO estimates, salinization of agricultural land will result in 30–50% land loss by the year 2050 if proper remedial measures are not taken on time.

Agricultural crops are adversely affected under salinity exhibiting a spectrum of responses ranging from poor growth, to decline in crop yields through alterations in soil physico-chemical and biological properties, to disturbance in the ecological balance of the region. Salinity has emerged as a major cause of land abandonment and aquifers for agricultural purposes and is a major factor for reduced crop productivity. The impacts of salinity include poor crop productivity, low monetary returns, and soil erosion (Hu and Schmidhalter 2002). Reduced crop productivities are caused by complex interactions among morphological, physiological, and biochemical processes through salinity-induced inadequate water and nutrient uptakes throughout the crop growth phase (Akbarimoghaddam et al. 2011; Singh and Chatrath 2001). Thus, the aim of the present chapter is to focus on halophilic microbe interactions with plants to mitigate salt stress.

12.2 Characteristics of Salt-Affected Soils

The presence of soluble salts in saline soils and high pH of the sodic soil differentiates them from arable soils. Soluble salts present in soils may affect crop production through changes in the amount of exchangeable cations, soil pH, physical properties, and the osmotic and specific ion toxicity. The substitution of exchangeable Na^+ with Ca^{2+} requires the application of amendment which may supply soluble Ca^{2+} ions directly or encourage the solubility of native calcium present in the soil. Nutrient imbalance or specific ion toxicity also adversely affects crop yields. On the basis of reclamation and management, the salt-affected soils of India can be categorized into alkali or sodic and saline soils. Alkali or sodic soils are those containing an excess of salts capable of alkaline hydrolysis like sodium carbonate, sodium bicarbonate, and sodium silicate and sufficient exchangeable sodium content to impart poor physical conditions to soil and affect the growth of most of the plants. pH in a saturated paste of these soils is greater than 8.5 with exchangeable sodium

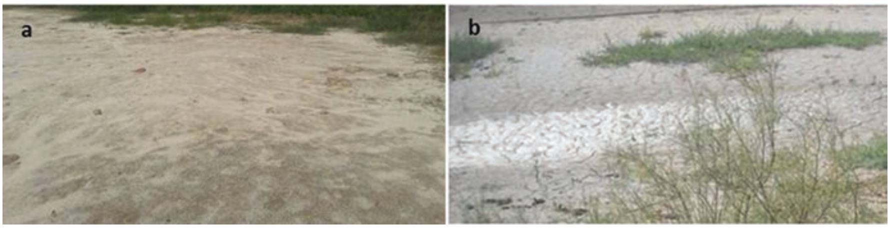

Fig. 12.1 Typical (**a**) alkali/sodic soil and (**b**) saline soil

percentage (ESP) of more than 15 and having different levels of salinity (electrical conductivity <4 dS m^{-1}). The presence of calcium carbonate in subsoil layers causes physical impedance for root proliferation (Fig. 12.1a).

Saline soils have generally encrustation of white salts on the surface layer that are predominantly chlorides and sulfates of Na^+, Ca^{2+}, and Mg^{2+}. These soils predominantly contain neutral soluble salts with pH of the saturation paste less than 8.5. The electrical conductivity of saturation extract (ECe) is greater than 4 dS m^{-1} at 25 °C. These soils always have a sodium absorption ratio (SAR) of the soil solution greater than 15. The occurrence of excessive neutral salts in soil restricts plant growth and development which is mainly due to the high osmotic pressure of soil solution and multifaceted interaction between sodium, calcium, and magnesium ions (Fig. 12.1b).

Imbalance in the uptake of mineral nutrients and their accumulation in the plant system is mainly due to salinity stress (Grattan and Grieve 1994). The most important and widely studied physiological impairments due to salt stress include osmotic stress; ion imbalances, particularly with Ca^{2+} and K^+; and direct toxic effects of Na^+ and Cl^- ions on the metabolic processes (Munns 2002, 2005). Soil salinity inhibits plant growth by affecting both water absorption and biochemical processes such as N and CO_2 assimilation and protein biosynthesis (Cusido et al. 1987). Under saline conditions, plants fail to maintain the required balance of organic and inorganic constituents leading to suppressed growth and yield (Gunes et al. 1996). Plant performance, usually expressed as crop yield, plant biomass, or crop quality, may be adversely affected by salinity-induced nutritional disorders. These disorders may be as a result of the effect of salinity on nutrient availability, competitive uptake, transport, or partitioning within the plant (Grattan and Grieve 1999; Zhu 2002; Nasim et al. 2008).

12.3 Microbial Ecology of Salt-Affected Soil

Microbial community in the soil is not distributed at random. Factors such as soil composition, organic matter, pH, water, and oxygen availability, along with the host plant, play a major role in the selection of the natural flora (Ross et al. 2000). The soil gains importance, especially in saline agriculture, where high soil salinity results from irrigation practices and application of chemical fertilizer. This effect is always more pronounced in the rhizosphere as a result of increased water uptake by the plants due to transpiration. Hence, the rhizobacteria form a group of the best adapted microorganisms (Tripathi et al. 1998). Saline or hypersaline soils have yielded many Gram-positive species, and these have been characterized taxonomically. The microbiota of hypersaline soils is more similar to those of non-saline soils than to the microbiota from hypersaline waters. This suggests that general environmental features are more important in determining the microbiota in a particular habitat than individual factors such as high salinity (Quesada et al. 1983).

Different enzymes of salt-tolerant microorganisms isolated from saline soils have been described in the recent past, and a number of new possibilities for industrial processes have emerged due to their inherent stability at high salt concentrations. These enzymes could be used in harsh industrial processes such as food processing, biosynthetic processes, and washing (Ventosa et al. 2005). Halophilic enzymes are active and stable at high salt concentrations, showing specific molecular properties that allow them to cope with osmotic stress. Organic compounds such as polyols, amino acids, sugars, and betaines are accumulated intracellularly by the halophilic and halotolerant bacteria to achieve osmotic balance (Brown 1976). Also, halophilic bacteria tolerant to heavy metals could be used as bioassay indicator organisms in saline-polluted environments (Rios et al. 1998).

12.4 Halophilic Microbes

Halophilic microorganisms or "salt-loving" microorganisms live in environments with high salt concentration that would kill most other microbes. The organisms found in salt-affected ecosystems have developed mechanisms to survive in such adverse conditions and many endemisms. Halophily refers to the ionic requirements for life at high salt concentrations. In hypersaline environments, halotolerant and halophilic microorganisms that grow as halophiles specifically need at least 0.2 M of salt for their growth. Halotolerant microbes can only tolerate a salt concentration of less than 0.2 M (~1%). The different categories of halophilic microorganisms are based on their level of salt requirement and salt tolerance. As per their response to the salt in which they grow, halophilic microbes have been classified into five groups: (1) non-halophilic, less than 0.2 M (~1%) salt; (2) slight halophiles, 0.2–0.5 M (~1–3%) salt; (3) moderate halophiles, 0.5–2.5 M (~3–15%) salt; (4) borderline extreme halophiles, 1.5–4.0 M (~9–23%) salt; and (5) extreme halophiles, 2.5–5.2 M (~15–32%) salt (Kushner 1993).

12.4.1 Diversity of Halophilic Microorganisms

Halophiles are found in each of the three domains: Archaea, Bacteria, and Eucarya. The metabolic diversity of halophiles is great as well; they include oxygenic and anoxygenic phototrophs, aerobic heterotrophs, fermenters, denitrifiers, sulfate reducers, and methanogens. The understanding of the biodiversity in salt-saturated environments has increased greatly in recent years. The soil bacteria play a role in the conservation and restoration biology of higher organisms. The domain Bacteria consists of many types of halophilic and halotolerant microorganisms that are spread over several phylogenetic groups (Ventosa et al. 1998). Among the cyanobacteria, the *Flavobacterium-Cytophaga* branch, the spirochetes, and the actinomycetes (Oren 2002) are also found as halophiles. Halophiles are found both within the aerobic branches (*Bacillus* and related organisms) and within the anaerobic branches. Generally most of the halophiles within the bacteria domain are moderate halophiles instead of extreme halophiles (Arahal and Ventosa 2002). However, there are a few types that resemble the archaeal halophiles of the family *Halobacteriaceae* in their salt requirements and tolerance. There was an abundance of halophilic bacteria in saline soil, with the dominant types encountered in saline soil belonging to the genera of *Alcaligenes*, *Bacillus*, *Micrococcus*, and *Pseudomonas* (Rodriguez-Valera 1988) (Table 12.1). Halotolerant Gram-positive endospore-forming rod-shaped bacteria were isolated from saline soils and sediments of salterns located in different parts of Spain belonging to the genus *Bacillus*. Of these bacteria majority of them were classified as extremely halotolerant microorganisms, being able to grow in salt concentration of 20–25% (Garabito et al. 1998).

Several alkaliphilic *Bacillus* species have been isolated from soil samples showing halophilic characteristics. *Bacillus krulwichiae*, a facultatively anaerobic (Yumoto et al. 2003), was isolated in Tsukuba, Japan. *Bacillus patagoniensis* and *Bacillus oshimensis* (Olivera et al. 2005; Yumoto et al. 2005) were also isolated from saline habitats. The genus *Virgibacillus* comprises eight species, two of which are moderately halophilic and have been isolated from soil samples: *Virgibacillus salexigens* (Garabito et al. 1997; Heyrman et al. 2003) and *Virgibacillus koreensis* (Lee et al. 2006). Genera that include halophilic species isolated from soil samples are *Halobacillus*, *Filobacillus*, *Tenuibacillus*, *Lentibacillus*, and *Thalassobacillus*. Species from *Filobacillus*, *Thalassobacillus*, and *Tenuibacillus* genera are borderline halophiles (Table 12.1). The genus *Halobacillus* is clearly differentiated from other related genera, and in these genera, the halophiles isolated from soils are *Halobacillus halophilus* (Spring et al. 1996) and *Halobacillus karajensis* (Amoozegar et al. 2003). Halophilic species from the genera *Lentibacillus*, *Nocardiopsis*, *Thermobifida*, and *Streptomonospora* were also isolated by workers. Some examples of moderately halophilic species of the genus *Nocardiopsis* isolated from soil samples are *Nocardiopsis gilva*, *Nocardiopsis rosea*, *Nocardiopsis rhodophaea*, *Nocardiopsis chromatogenes*, and *Nocardiopsis baichengensis* (Li et al. 2006). These are all isolated from saline sediment from Xinjiang Province, China. From salt pans of Kovalam in Kanyakumari district of Kerala, India, Gram-negative moderately halophilic bacteria like *Natranobacterium sp-1.* identified in the study of the diversity over a period of time (Murugan et al. 2011). Many Gram-negative, moderately halophilic, or halotolerant species are currently included in the family *Halomonadaceae* (Arahal and Ventosa 2005). This family includes three genera with halophilic species: *Halomonas*, *Chromohalobacter*, and *Cobetia*.

Several strains were isolated from saline soils and described as new species belonging to the genus *Halomonas*: *Halomonas maura* (Bouchotroch et al. 2001)

Table 12.1 Halophiles isolated from soils and sediments

Species	Isolation source	References
Moderate halophiles (3–15%)		
Bacillus krulwichiae	Soil from Tsukuba, Ibaraki, Japan	Yumoto et al. (2003)
Bacillus haloalkaliphilus	Showa, Saitama	Echigo et al. (2005)
Bacillus oshimensis	Soil from Oshymanbe, Oshima, Hokkaido, Japan	Yumoto et al. (2003)
Bacillus patagoniensis	Rhizosphere of *Atriplex lampa*, North-eastern Patagonia, Argentina	Olivera et al. (2005)
Gracilibacillus halotolerans	Shiki, Saitama	Echigo et al. (2005)
Halobacillus halophilus	Salt marsh and saline soils	Spring et al. (1996), Ventosa et al. (1983)
Halobacillus karajensis	Saline soil of Karaj region, Iran	Amoozegar et al. (2003)
Halomonas anticariensis	Soil from Fuente de Piedra. Málaga, Spain	Martínez-Cánovas et al. (2004a)
Halomonas boliviensis	Soil around the lake Laguna Colorada, Bolivia	Quillaguaman et al. (2004)
Halomonas maura	Soil from a solar saltern, Asilah, Morocco	Bouchotroch et al. (2001)
Halomonas organivorans	Saline soil from Isla Cristina, Huelva, Spain	Garcia et al. (2004)
Lentibacillus salaries	Saline sediment of Xinjiang Province, China	Jeon et al. (2005a)
Lentibacillus salicampi	Salt field in Korea	Yoon et al. (2002)
Marinobacter excellens	Sediment from Chazhman Bay, Sea of Japan	Gorshkova et al. (2003)
Marinobacter koreensis	Sea sand in Pohang, Korea	Kim et al. (2006)
Marinobacter lipolyiticus	Saline soil from Cadiz, Spain	Martin et al. (2003)
Marinobacter sediminum	Marine coastal sediment from Peter the Great Bay, Sea of Japan	Romanenko et al. (2005)
Microbacterium halotolerans	Soil sediment of Qinghai Province, China	Li et al. (2005a)
Natranobacterium sp-1	Salt pan, Kovalam, India	Murugan et al. (2011)
Nocardiopsis baichengensis	Saline sediment from Xinjiang Province, China	Li et al. (2006)
Nocardiopsis chromatogenes	Saline sediment from Xinjiang Province, China	Li et al. (2006)
Nocardiopsis gilva	Saline sediment from Xinjiang Province, China	Li et al. (2006)
Nocardiopsis rhodophaea	Saline sediment from Xinjiang Province, China	Li et al. (2006)
Nocardiopsis rosea	Saline sediment from Xinjiang Province, China	Li et al. (2006)
Palleronia marisminoris	Hypersaline soil of a solar saltern in Murcia, Spain	Martinez-Checa et al. (2005)
Salipiger mucosus	Hypersaline soil of a solar saltern in Calblanche, Murcia, Spain	Martinez-Canovas et al. (2004b)

(continued)

Table 12.1 (continued)

Species	Isolation source	References
Salipiger mucosus	Hypersaline soil of a solar saltern in Calblanche, Murcia, Spain	Martinez-Canovas et al. (2004b)
Virgibacillus halodenitrificans	Ranzan, Saitama	Echigo et al. (2005)
Virgibacillus koreensis	Salt field near Taean-Gun on the Yellow Sea in Korea	Lee et al. (2006)
Borderline halophiles (9–23%)		
Actinopolyspora iraqiensis	Soil sample in Iraq	Ruan et al. (1994)
Actinopolyspora mortivallis	Soil from Death Valley, California, USA	Yoshida et al. (1991)
Alkalibacillus haloalkaliphilus	Alkaline, highly saline mud from Wadi Natrun, Egypt	Jeon et al. (2005b)
Alkalibacillus salilacus	Soil sediment from a salt lake in Xinjiang Province, China	Jeon et al. (2005b)
Bacillus megaterium	Kasukabe, Saitama	Echigo et al. (2005)
Filobacillus milosensis	Beach sediment from Palaeochori Bay, Milos, Greece	Schlesner et al. (2001)
Filobacillus milosensis	Okabe, Saitama	Echigo et al. (2005)
Halobacillus karajensis	Katsushika, Tokyo	Echigo et al. (2005)
Halobacillus litoralis	Okegawa, Saitama	Echigo et al. (2005)
Halobacillus salinus	Salt pan, Kovalam, India	Murugan et al. (2011)
Halobacillus tueperi	Omiya, Saitama	Echigo et al. (2005)
Halobacterium salinarum	Salt pan, Kovalam, India	Murugan et al. (2011)
Halococcus salifodinae	Salt pan, Kovalam, India	Murugan et al. (2011)
Lentibacillus salicampi	Iwatsuki, Saitama	Echigo et al. (2005)
Saccharomonospora paurometabolica	Saline sediment of Xinjiang Province, China	Li et al. (2003)
Staphylococcus citreus	Salt pan, Kovalam, India	Murugan et al. (2011)
Staphylococcus epidermidis	Salt pan, Kovalam, India	Murugan et al. (2011)
Staphylococcus intermedius	Salt pan, Kovalam, India	Murugan et al. (2011)
Tenuibacillus multivorans	Soil from Xinjiang Province, China	Ren and Zhou (2005)
Thalassobacillus devorans	Saline soil in South Spain	García et al. (2005)
Vibrio fischeri	Salt pan, Kovalam, India	Murugan et al. (2011)
Extreme halophiles (15–32%)		
Bacillus subtilis	Salt pan, Kovalam, India	Murugan et al. (2011)
Marinococcus halophilus	Saline soil from Alicante and Cadiz, Spain	Hao et al. (1984), Marquez et al. (1992)
Marinococcus halotolerans	Saline soil in Qinghai, north-west China	Li et al. (2005b)

and *Halomonas anticariensis* (Martinez-Canovas et al. 2004a). Other halophilic EPS-producing species were also isolated in these studies: *Salipiger mucosus*, which was the first moderately halophilic EPS-producing microorganism belonging to *Alphaproteobacteria* (Martinez-Canovas et al. 2004b). The genus *Marinobacter* accommodates moderate halophile species *Marinococcus halophilus* and *Marinococcus albus* (Hao et al. 1984). *Marinococcus halotolerans* are extremely halophilic motile cocci that grow over a wide range of salt concentrations and up to 20% NaCl (Li et al. 2005b). The genus *Marinobacter* comprises 13 species, some of which are moderately halophilic bacteria isolated from soil samples: *Marinobacter lipolyticus*, which shows lipolytic activity with potential industrial applications (Martin et al. 2003), *Marinobacter excellens* (Gorshkova et al. 2003), *Marinobacter sediminum* (Romanenko et al. 2005), and *Marinobacter koreensis* (Kim et al. 2006) (Table 12.1). Gram-positive bacteria like *Halobacillus salinus*, *Staphylococcus epidermidis*, *Staphylococcus intermedius*, and *Staphylococcus citreus* were isolated from salt pans of Kovalam in Kanyakumari district of Kerala, India, while Gram-negative organisms like *Vibrio fischeri*, *Halobacterium salinarum*, and *Halobacterium salifodinae* were identified in the study of the diversity over a period of time (Murugan et al. 2011).

12.4.2 Halophilic Endophytes

Endophytic microorganisms are those that thrive inside the plants. These organisms face less competition for nutrients and are more protected from unfavorable changes in the environment than the bacteria in the rhizosphere and phyllosphere as they interact directly with the host plants (Weyens et al. 2009). They may also help in degradation of the pollutants taken by the plants, thus lowering the phytotoxic effect. Halophilic endophytic bacteria were isolated from the leaves of dominant halophyte plant species dominant in the coastal ecosystem of the west coast of India and were assessed for their plant growth promotion traits (Arora et al. 2014a; Arora and Vanza 2017). Evidences indicate that endophytes can contribute to the phytoremediation of intractable organic and inorganic contaminants including heavy metals (Thijs et al. 2014; Becerra-Castro et al. 2013). The endophytic bacteria can enhance plant growth either directly by producing auxins and cytokinins or by enhancing the availability of nutrients through a number of biochemical processes like nitrogen fixation, phosphate solubilization, and siderophore production or indirectly through the suppression of ethylene production by 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase, chemical induction of plant defense mechanisms, or degradation of harmful contaminants (Thijs et al. 2014; Weyens et al. 2009). Therefore endophytic microbes are suitable for application in bioremediation for salt and drought stress.

12.4.3 Halotolerance Mechanism

Halotolerance is the adaptation of living organisms to conditions of high salinity. High osmolarity in hypersaline conditions can be deleterious to cells since water is lost to the external medium until osmotic equilibrium is achieved. Many microorganisms respond to increase in osmolarity by accumulating osmotica in their cytosol, which protects them from cytoplasmic dehydration (Yancey et al. 1982). As biological membranes are permeable to water, all microorganisms have to keep their cytoplasm at least isosmotic with their environment to prevent water loss of cellular water; when turgor pressure is to be maintained, the cytoplasm should even be slightly hyperosmotic. Adaptation to conditions of high salinity has an evolutionary significance. Osmophily is related to the osmotic aspects of life at high salt concentrations, especially turgor pressure, cellular dehydration, and desiccation.

In general, halophilic microorganisms adopt either of the two strategies for survival in saline environments: (a) "compatible solute" strategy and (b) "salt-in" strategy (Ventosa et al. 1998). When an isosmotic balance within the medium is achieved, the cell volume is maintained. The majority of moderately halophilic and halotolerant bacteria, some yeasts, algae, and fungi employs the strategy of compatible solute wherein cells maintain low concentrations of salt in the cytoplasm by balancing osmotic potential through the synthesis or uptake of organic compatible solutes and exclusion of salts from the cytoplasm. In halophiles, the compatible solutes or osmolytes, small organic molecules that are soluble in water, accumulate and are available in a great spectrum that is used in all three domains of life. These are mainly assigned in the following two classes: (1) amino acids and their derivatives, such as glycine, betaine, glutamine, glutamate, proline, ectoine, or N-acetyl-β-lysine, and (2) polyols such as glycine betaine, ectoine, sucrose, trehalose, and glycerol, which does not disrupt metabolic processes and does not have net charge at physiological pH. The accumulation can either be accomplished by uptake from the medium or by de novo synthesis (Shivanand and Mugeraya 2011).

True halophiles, including halophilic archaea and extremely halophilic bacteria, employ the salt-in strategy. These microorganisms are adapted to high salt concentrations but cannot survive when the salinity of the medium is lowered (Arora et al. 2014b) as they generally are unable to synthesize organic solutes for maintaining the osmotic equilibrium. In this adaptation mechanism, the intracellular K^+ and Na^+ concentrations are normally higher and lower, respectively, than that of the outside or in the medium. The intracellular K^+ concentration increases non-linearly with increasing external NaCl concentration. All halophilic microorganisms contain potent transport mechanisms, generally based on Na^+/H^+ antiporters (Oren 1999).

The first chloride-dependent bacterium reported was *Halobacillus* having several cellular functions depending on Cl^- for maximal activities, the most important being the activation of solute accumulation. Production of different compatible solutes by *Halobacillus* helps in switching its osmolyte strategy with the salinity in its environment. Glutamate and glutamine dominate at intermediate salinities, and proline and ectoine dominate at high salinities where chloride stimulates expression of the glutamine synthetase and activates the enzyme. The product glutamate then turns on the biosynthesis of proline by inducing the expression of the proline biosynthetic genes. *Halobacillus dabanensis* is used as a model organism to study the genes involved in halotolerance, including genes encoding Na^+/H^+ antiporters, enzymes involved in osmotic solute metabolism, and stress proteins. The higher proline content generated in response to elevated salinity has also been reported as a powerful antioxidant in managing oxidative adjustments and protects intracellular macromolecules under high osmotic stress conditions (Upadhyay and Singh 2015). Exopolysaccharides play an important role in the formation and stabilization of soil aggregates as well as nutrient and water flow regulation across the plant roots (Ashraf et al. 2006). It has been reported that there is increase in root growth of wheat plants when inoculated with exopolysaccharide-producing bacteria, and this increased root growth helps in overcoming the negative effects of soil salinity through enhanced soil water uptake, restricting Na^+ influx in plants and accelerating soil microbial process involved in cycling and nutrient availability to plants under salt stress.

12.5 Mycorrhizal Fungi for Mitigating Salt Stress

Mycorrhiza is a specialized fungi belonging to the order Glomerales that colonize plant roots and extend far into the soil. More than 90% of plant species form a symbiotic relationship with the beneficial mycorrhizal fungi. There are two types of mycorrhiza: arbuscular mycorrhizae (AM) and ectomycorrhizae (ECM); both are differentiated on the basis of their associations with plants. AM fungi are most abundantly found in agricultural fields. AM fungal associations comprise three main structures: (a) hyphae work as external filamentous arms searching for nutrients around the root zone (Hodge 2000); (b) there are specialized vesicles within the root, which are thought to be storage organs, especially for lipids (Hirsch and Kapulnik 1998); and (c) arbuscules are the third important part of the AM association. These arbuscules are responsible for the exchange of nutrition and metabolites between fungus and host plant. The AM fungal hyphae also proliferate into the soil which helps the plants to absorb mineral nutrients and water from the soil. These fungal hyphae present in soils also improve soil porosity and structure.

Mycorrhizal association demonstrates several growth-promotion properties by several mechanisms. These mechanisms include production of several plant growth-promoting metabolites like amino acids, vitamins, and phytohormones. Mycorrhiza also has nutrient solubilizing and mineralizing potential (Evelin et al. 2009; Kumar et al. 2015). Several researchers have reported that mycorrhizal fungi can enhance plant tolerance against various stresses like drought and salinity (Beauchamp et al. 2009). Hence they can help in improving crop growth and yield. Along with providing nutritional and structural advantages to plants, they also provide other benefits like production and accumulation of secondary metabolites around the roots and also help in osmotic adjustment in osmotic stress, facilitate nitrogen fixation, enhance photosynthesis rate, and increase resistance against biotic and abiotic stresses (Hashem et al. 2015). It has been documented in several studies that mycorrhiza also enhances nutrient uptake in salt stress (Chang et al. 2018). Vesicular-arbuscular mycorrhizal fungi commonly called VAM occur naturally in saline environment.

The most commonly observed VA mycorrhizal fungi in saline soils are *Glomus* spp. (Juniper and Abbott 1993), suggesting that this species may be adapted to grow under saline conditions, but ecological specificity has not been demonstrated. There are evidences that with increased salinity, VAM species distribution markedly changes (Stahl and Williams 1986). In the severely saline soils of the Tabriz plains, Aliasgharzadeh et al. (2001) observed that the most predominant species of arbuscular mycorrhizal fungi (AMF) were *Glomus intraradices*, *G. versiform*, and *G. etunicatum*. Some studies indicate that mycorrhizal fungi can increase growth of plants growing in saline habitats (Yadav et al. 2017). These studies thus advocate that VA mycorrhizal fungi have the ability to protect plants from salt stress. Several researchers investigated the relationship between soil salinity and occurrence of mycorrhizae on halophytes. It has been reported that the number of VAM spores or infectivity of VAM fungi changed with change in salt concentration (Juniper and Abbott 1993). The salinity stress affects the growth of plants, fungus, or both. These findings suggest that the capability of AMF in protecting plants from the detrimental effects of salt stress may depend on the behavior of each species.

12.6 Microbes Enabling Mitigation of Salt Stress in Plants

Bacteria and fungi have been identified that can improve plant yields in these stressed environments. The bacterial genera that have been implicated in these benefits include *Rhizobium*, *Bacillus*, *Pseudomonas*, *Pantoea*, *Paenibacillus*, *Burkholderia*, *Achromobacter*, *Azospirillum*, *Microbacterium*, *Methylobacterium*, *Variovorax*, and *Enterobacter* (Barassi et al. 2006; Dodd and Perez-Alfocea 2012; Grover et al. 2010; Nia et al. 2012; Ramadoss et al. 2013; Selvakumar et al. 2009; Upadhyay et al. 2009; Yang et al. 2009; Yildirim and Taylor 2005). Some of these organisms are capable of activating systemic changes in plants that confer tolerance to abiotic stress; this phenomenon has been termed "induced systemic tolerance" (Yang et al. 2009). Many studies have shown that under conditions of environmental stress, microbial inoculants that promote plant root growth provide measurable benefits to plant growth and/or plant health (Arora et al. 2017). In particular, inoculation of plants with various PGPRs has been shown to enhance the formation of lateral roots and root hairs (Paul and Lade 2014) and roots with larger root surface area (Diby et al. 2005; Paul and Sarma 2006). A major mechanism by which bacteria can influence plant root system development is through the production of the auxin indole-3-acetic acid (IAA). This phytohormone is a major hormone used by plants to regulate growth. It is involved in a breadth of physiological processes including plant cell division and differentiation, germination, vascular development, and root growth. The contribution of IAA production to root growth under environmentally stressful conditions has been identified with other microbes. Sadeghi et al. (2012) demonstrated that a *Streptomyces* isolate produced IAA and promoted the growth of wheat under high salinity conditions. Similarly, Yao et al. (2010) found that an IAA-producing *Pseudomonas putida* strain promoted the growth of cotton seedlings under high salinity conditions. The finding that this *P. putida* strain also inhibited production of the stress-inducible phytohormone abscisic acid illustrates the complexity of elucidating mechanisms underlying plant growth promotion. The benefits of IAA production by PGPR may be augmented by the production of an enzyme, ACC deaminase (Etesami et al. 2014, 2015a, b). Bacteria can produce other phytohormones as well, including cytokinins (Arkhipova et al. 2007) and gibberellins (Bottini et al. 2004), which may contribute to plant growth under stressful conditions (Arkhipova et al. 2007).

Plants respond to a variety of stresses by accumulating ethylene, and this accumulation can inhibit root development. By decreasing ACC levels in plants, ACC deaminase-producing microorganisms decrease plant ethylene levels and alleviate this inhibition (Glick et al. 2007). Plants inoculated with ACC deaminase-producing bacteria, or expressing a bacterial ACC deaminase transgene, develop a more extensive root system and exhibit enhanced tolerance to environmental stresses (Arshad et al. 2007; Safronova et al. 2006; Stearns et al. 2005). Although a diversity of bacteria and fungi express ACC deaminase, this activity has been studied most extensively in PGPRs (Glick 2005), including the genera *Achromobacter*, *Acidovorax*, *Alcaligenes*, *Enterobacter*, *Klebsiella*, *Methylobacterium*, *Pseudomonas*, *Rhizobium*, and *Variovorax* (Esquivel-Cote et al. 2010). Bacteria in the symbiotic nitrogen-fixing genus *Bradyrhizobium* can also reduce ethylene accumulation in plants.

Plant nutrient deficiency under stress can also exacerbate the adverse effects of other abiotic stresses (Baligar et al. 2001; Grieve and Grattan 1999; Khoshgoftarmanesh et al. 2010). Studies showed that plants exposed to environmental stresses require additional supplies of mineral nutrients to minimize the adverse effects of stress (Endris and Mohammad 2007; Heidari and Jamshid 2010; Kaya et al. 2002). The best characterized mutualistic interactions in the rhizosphere, namely, the AMF- and symbiotic nitrogen-fixing bacteria-plant interactions, help plants overcome nutrient deficiencies that are incurred in soils with low fertility (Glick 2012). PGPRs can enhance the availability of these nutrients by increasing their solubility or uptake.

12.7 Halophilic Bacteria for Bioremediation of Salt-Affected Soils

Both physical and chemical methods for reclamation of salt-affected soils are not cost-effective, and also the availability of mineral gypsum or other chemical amendments is a scarce. The applications of halophilic bacteria include recovery of salt-affected soils by directly supporting the growth of vegetation, thus indirectly increasing crop yields in salt-affected soils. All halophilic microorganisms contain potent transport mechanisms, generally based on Na^+/H^+ antiporters, to expel sodium ions from the interior of the cell (Oren 2002). Also, some halophiles express ACC deaminase activity that removes stress and ethylene from the rhizosphere, and some produce auxins that promote root growth. Halophilic microbes are also found to remove salt from saline soils (Bhuva et al. 2013). There are reports that potential salt-tolerant bacteria isolated from soil or plant tissues and having plant growth promotion trait help to alleviate salt stress by promoting seedling growth and increasing biomass of crop plants grown under salinity stress (Chakraborty et al. 2011; Arora et al. 2013; Arora et al. 2014b).

12.7.1 Halophilic Bacteria for Plant Growth Under Salt Stress

To overcome the salinity problems, the biotic approach "plant-microbe interaction" has recently received considerable attention globally. The plant-microbe interactions are beneficial associations between plants and microorganisms and can also be a more efficient method for the reclamation or amelioration of salt-affected soils. Although salt shows negligible effects on seed germination and seedling growth, salt sensitivity of many crops is well documented on plant dry weight and biomass as the major energy of the plant is utilized to maintain osmotic balance under salt stress (Jamal et al. 2011; Saqib et al. 2012). Plant growth-promoting rhizobacteria-induced plant salt stress tolerance has been well studied and is considered to be a cost-effective solution to the problem. PGPR isolated from saline soils improves plant growth at high salt concentration (Mayak et al. 2004; Yildirim and Taylor 2005; Barassi et al. 2006).

These halophilic plant growth-promoting rhizobacteria tolerate a wide range of salt stress and enable plants to withstand salinity by hydraulic conductance, osmotic accumulation, sequestering toxic Na^+ ions, and maintaining higher osmotic conductance and photosynthetic activities (Dodd and Perez-Alfocea 2012). The inoculation with halophilic strains of plant growth-promoting rhizobacteria helps to improve the stress tolerance of plants especially salinity stress and promote growth of food crops which is essentially required to meet the food demands of the country.

It was reported that aminocyclopropane-1-carboxylic acid (ACC) deaminase-containing halotolerant strain SAL-15 (*Planococcus* spp.) which is also an indole acetic acid (IAA)-producing strain increased root and shoot growth and plant biomass under salt stress in the presence of ACC. Inoculated plants showed 71% increase in plant weight, 94% in root length, and 183% in shoot length than un-inoculated control plants. In the presence of salt, bacteria showing IAA activity without ACC deaminase activity inhibit root growth rather than root elongation showing the importance of and higher synthesis of ACC under stress (Cheng et al. 2007). ACC deaminase-containing plant growth-promoting *Enterobacter* sp. was found to be an effective bioresource for inducing salt tolerance and consequent improvement in the growth of okra plants under salt stress (Habib et al. 2016).

Plant growth-promoting rhizobacteria assist in diminishing the accumulation of ethylene levels and re-establish a healthy root system required to cope with environmental stress. The primary mechanism includes the destruction of ethylene via enzyme ACC deaminase. Rhizosphere bacteria such as *Achromobacter*, *Azospirillum*, *Bacillus*, *Enterobacter*, *Pseudomonas*, and *Rhizobium* with ACC deaminase activity help in alleviating stress (Ghosh et al. 2003; Govindasamy et al. 2008; Duan et al. 2009). Many of the studies have demonstrated the production of ACC deaminase gene in plants treated with plant growth-promoting rhizobacteria under environmental stress. Grichko and Glick (2001) inoculated tomato seeds with *Enterobacter cloacae* and *Pseudomonas putida* expressing ACC deaminase activity and reported an increase in plant resistance. Ghosh et al. (2003) recorded ACC deaminase activity in three *Bacillus* species, namely, *Bacillus circulans* DUC1, *Bacillus firmus* DUC2, and *Bacillus globisporus* DUC3, which stimulated root elongation in *Brassica campestris*. Mayak et al. (2004) observed tomato plants inoculated with the bacterium *Achromobacter piechaudii* under water and saline stress conditions and reported a significant increase in fresh and dry weight of inoculated plants. Many rhizobia isolated from Acacia, such as *Sinorhizobium arboris*, turned out to be moderately salt tolerant, capable of growing in 0.3–0.5 M (2–3%) NaCl (Zahran et al. 1994). IAA-producing bacteria *Kocuria turfanensis* isolated from the rhizospheric soil of halotolerant plant *Suaeda fruticosa* was reported to increase the length of the groundnut plant and fresh biomass (Goswami et al. 2014). On dual inoculation with *Pseudomonas* sp. and *Bacillus cereus*, it was observed that the levels of IAA and ABA were increased in leaves of wheat growing in saline soil (Ul-Hassan and Bano, 2014). Phototrophic bacterium *Rhodopseudomonas palustris* increased growth and induced systemic resistance in cucumber seedlings under salt stress by the production of IAA, ALA, and soluble sugars, the induction of antioxidant enzymes, as well as nutrient adjustment of N, P, and K (Ge and Zhang 2018). Jha and Subramanian (2013) found a potential effect of some osmotolerant bacteria on the germination of paddy seeds under saline conditions. This is attributed to IAA production by inoculated bacteria, which plays an important role in the germination of seeds. Exopolysaccharide-producing bacteria provided a “blanket salt-tolerant cover” on the roots by increasing soil aggregation around roots (Ashraf et al. 2006) and also enhancing the volume of soil macropores that results in increased water and fertilizer availability to the inoculated plants (Upadhyay et al. 2011). Mohammed (2018) reported that the activities of biofilm formation and exopolysaccharide production of the strain *Pseudomonas anguilliseptica* at different salt concentrations enhanced plant height and fresh and dry weight of faba bean plants.

Plant growth-promoting rhizobacteria including *Rhizobium*, *Pseudomonas*, *Acetobacter*, *Bacillus*, and *Flavobacterium*, and several *Azospirillum* can maintain their plant growth-promoting ability even at high saline conditions. It has been demonstrated that *Azospirillum* inoculation mitigates the negative effects of NaCl on plant growth parameters, and this beneficial effect of *Azospirillum* inoculation was observed in wheat seeds, where the mitigating effect of salt stress was evident (Creus et al. 1997). Wheat (*T. aestivum*) seedlings after inoculation with *Azospirillum* subjected to osmotic stress developed significantly higher coleoptiles, with higher fresh weight and better water status than un-inoculated seedlings (Creus et al. 1998). From saline coastal ecosystem, plant growth-promoting halophilic bacterial strains (CSSRO2 *Planococcus maritimus*) and CSSRY1 (*Nesterenkonia alba*) were isolated from the rhizosphere soil of dominant halophytes (Arora et al. 2012). It was observed that inoculation of strain CSSRY1 decreased soluble sodium content up to 31% at 4% NaCl concentration while at 10% NaCl concentration, it reduced only 19% sodium from the soil. In pot experiments with wheat, there was increase in plant growth parameters and yield of wheat when halophilic bacteria were inoculated with seeds under saline water irrigation. There was 10–12% increase in yield attributes and yield of wheat with 6% NaCl compared to un-inoculated (Fig. 12.2). Under salt stress, consortium of halophilic bacteria inoculation with *Zea mays* seeds showed growth up to 10% NaCl, whereas inoculation with single isolate did not promote plant growth at this salt concentration. The maximum fresh weight, dry weight, shoot length, and root length of plants were found in the case of "Consortium 5% NaCl" treated pot, 194.5% increase in fresh weight, 98.97% increase in dry weight, 15.37 cm increase in shoot length, and 7.4 cm increase in root length compared to the un-inoculated control plants (Fig. 12.3) (Arora et al. 2013). The result indicated that inoculation with halophilic bacterial isolates can promote the growth of plants in saline soils due to the production of hormone auxin and thus enhanced

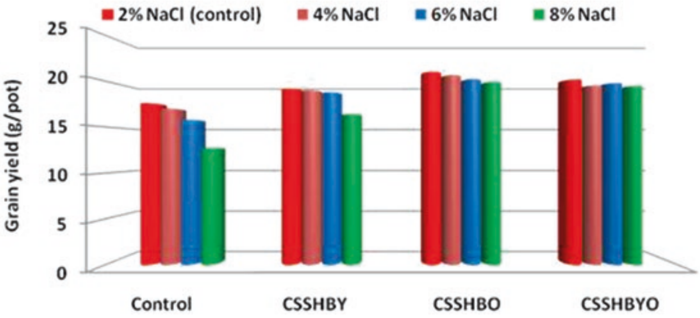

Fig. 12.2 Performance of wheat at different salinity stresses inoculated with halophilic bacteria

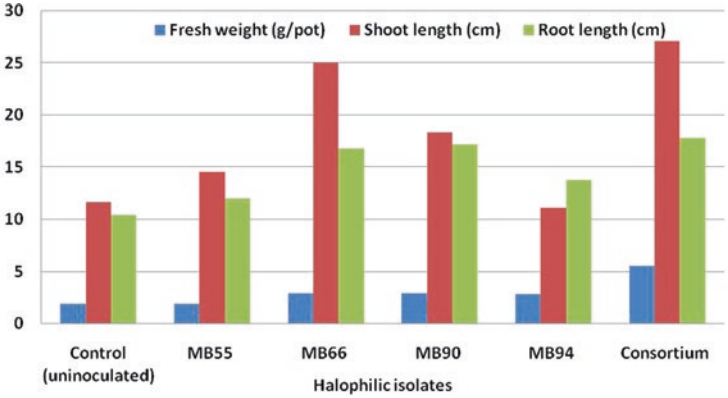

Fig. 12.3 Growth performance of *Zea mays* inoculated with halophilic bacteria at 5% salinity stress

Fig. 12.4 Liquid bioformulations: Halo-Azo and Halo-PSB

root growth. Another very likely mechanism may be the alleviation of salinity stress via expression of ACC deaminase activity by this plant growth-promoting rhizobacteria (PGPR). This enzyme is known to remove stress ethylene from the rhizosphere. Also, the halophilic/halotolerant bacteria remove sodium from the surrounding soil and are useful in plant growth promotion in salt-affected soils. Also, salt-tolerant rhizobium species were isolated from coastal saline soils (Trivedi and Arora 2013), which were able to enhance plant growth under salt stress (Fig. 12.4).

Halophilic microbes were found to have the ability to remediate the saline soil and can be used for glycophytes or crop plants for optimum growth under saline condition.

Similarly, for bioremediation of sodic soil of Indo-Gangetic plains, halophilic plant growth-promoting bacteria were isolated from native sodic soil of high pH and were screened for salt tolerance and plant growth-promoting traits. The efficient halophiles among N-fixers and P-solubilizers were tested for crop production at different soil pH and were prepared as liquid bioformulations “Halo-Azo” and “Halo-PSB” (Arora et al. 2016). These bioformulations were either used for seed/seedling treatment or soil application. It has been reported that co-inoculation of liquid bioformulations ‘Halo-Azo’ and ‘Halo-PSB’ in rice under sodic conditions resulted in higher yield and improvement in soil properties (Sahay et al. 2018).

Application of these bioformulations helps to supplement plant nutrients like nitrogen and phosphorous through their activities in the rhizosphere and make them available to plants in a gradual manner under salt stress. It ensures better root development and better nutrient uptake and thereby vigorous crop growth. Application of organic manures and/or compost along with liquid bioformulations “Halo-Azo” and “Halo-PSB” was found to be effective to significantly enhance yield of rice and wheat crops by an average of 11.5% on sodic soils up to soil pH 9.8. These are also effective in mustard, vegetable, and fodder crops under sodic stress. These formulations also help in the maintenance of soil health, minimize environmental pollution, and reduce the use of chemicals to some extent. They are affordable for most farmers who are small and marginal. Bioformulations are also ideal input for reducing the cost of cultivation and promoting organic farming in salt-affected soils.

12.8 Conclusions and Future Prospects

The identified halophilic plant growth-promoting microbes need to be applied in agriculture to enhance crop yields under salt stress conditions. Preparation of biological formulations based on beneficial halophiles can extend the range of options for enhancing growth and yield of crops in saline habitat. A new approach has been developed recently to alleviate salt stress in plants by inoculating crop seeds and seedlings with salt-tolerant plant growth-promoting microbes. Thus, there is great opportunity for halophilic PGPR for their successful application in agriculture. The microbial formulation and application technology are crucial for the development of commercial salt-tolerant bioformulation effective for plant growth under salt stress conditions. Bioformulations offer an environmentally sustainable approach to increase crop production and maintenance of soil health. Apart from bioformulation, reclamation and improving fertility of salt-stressed soils through the use of halophiles are other aims to be focused on. It has been observed that inoculation with mixed strains or consortia was more consistent than single-strain inoculations. Studies on the detailed mechanism of mycorrhizal fungi-associated plant growth under salt stress are lacking, and this needs to be explored. To tackle the problem of soil salinity, a promising approach includes utilizing beneficial microorganisms like PGPR that will make the greatest contribution to the agricultural economy as they can provide cheap and eco-friendly technique to mitigate salt stress.

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Effect of Salinity on Soil Nutrients and Plant Health

13

Ankita Bidalia, Krati Vikram, Gupta Yamal, and K. S. Rao

Abstract

Salinity is one of the most studied abiotic factors affecting soil and plant health in most of the arid and semiarid ecosystems across the globe. It affects the soil by altering the physical, chemical, and biological properties such as soil pH, bulk density, nutrient imbalance, moisture availability, and microbial diversity. These changes in the soil properties further affect the plant health by creating unfavorable conditions like osmotic stress, ion toxicity, low nutrient bioavailability, altered plant-pathogen interactions, etc. However, in natural conditions, both biotic and abiotic factors interact; therefore, plants have to defend themselves against multiple stresses simultaneously. Remarkably, plants have developed a variety of mechanisms to survive under the stressful condition with an alteration in the different plant processes. The aim of this chapter is to provide an overview of salinity imbalance soil nutritional and microbial status on plant health and also summarize the appropriate management practices to overcome salinity conditions.

Keywords

Nutrient bioavailability · Plant-pathogen interaction · Soil management

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13.1 Introduction

Salinity affects 20% of the world's irrigated land and approximately 30% of the arid and semiarid regions of the world (Newer et al. 2013). It is an important constraint to the world agriculture, affecting 7% of the land surface of the earth and over 50% of irrigated land, in particular where the salt concentration can be close to seawater (Flowers et al. 1977; Kalaji and Nalborczyk 1991; Shannon 1997). The process of enrichment of soil with the soluble salts is known as soil salinization (Asfaw et al. 2018). The sources of salinity can be categorised as natural (Primary) and anthropogenic (secondary) for e.g., the intrusion of salinized water in coasts, continental (fossil salt aquifers), Aeolian, dissolution of parent minerals and fertigation, application of inorganic/organic soil amendments) respectively. Saline soil can be categorized depending on the content of dissolved salts (cations/anions) such as sodic, saline-sodic, etc. (Ondrasek et al. 2011). Soil with excessive salt concentration imparts a detrimental impact on soil microbial population as well as their activities such as a decrease in carbon dioxide production, enzyme activities, or microbial biomass. The abovementioned microbial processes are also used frequently to determine soil quality. Soil microorganisms have developed the ability to withstand the osmotic stress caused by salinity, but still, there is limited information related to the effects of salt on soil biological activity (Saviozzi et al. 2011).

Salinity is a natural part of our earth, and many organisms show an adaptive mechanism toward saline conditions (Garg and Gupta 2011). Uptake of nutrients by plants is essential for their proper growth and development. However, interestingly the presence of the essential nutrients in the soil is no guarantee for the availability of nutrients to growing plants. In saline soils, there is a preponderance of nonessential elements over essential elements, and the plants face the challenge of absorption of essential nutrients as they are diluted in the concentrated nonessential nutrients. As a result of the competitive process between nutrients and major salt species, the uptake and accumulation of nutrients by plants are often reduced under saline conditions. In addition to this challenge, the plants also face toxic effect due to the high concentration of ions and an increase in osmotic potential of the rhizosphere. Thus, salinity and mineral nutrition interaction is very complex (Grattan and Grieve 1992). The present chapter focuses on the effect of salinity on soil nutritional balance, microbial status, and how it affects the overall plant health and also on the appropriate management practices to overcome salinity conditions in the soils.

13.2 Effect of Salinity on Soil Nutrients

The presence of dissolved salts in the soil profile due to soil salinization leads to an impairment in food production, socioeconomic well-being, and environmental health (Ondrasek et al. 2011). The interaction between soil salinity and mineral nutrition is very complex. The interaction depends on the level of salinity and the concentration of nutrients and is also influenced by plant characters (such as species, genotype, age) and climatic conditions. The saline conditions, which are characterized by low nutrient-ion activities, further affect plant nutrition and growth (Grattan and Grieve 1992). Nutrients can be micronutrients and macronutrients depending on the quantity in which they are required by the plants. Here, we will discuss the interaction of salinity with few important macronutrients, viz., nitrogen, phosphorous, and potassium (also known as primary nutrients), whose unavailability/scarcity in the absorbable form pose the highest degrees of limitation to crop growth and yield.

13.2.1 Interaction of Salinity with Nitrogen

Nitrogen accounts for about 80% of total mineral nutrients. Under salt stress, its availability is most widely limiting for plant growth and production. It has been observed that the interaction between salinity and nitrogen is generally conducted on soils that were deficient in N. Therefore, in crops like wheat, corn (Soliman et al. 1994), millet, cotton, and rice (Grattan and Grieve 1999), N application improved the growth or yield of the plants, whereas similar results were not obtained in the case of Sorghum under extremely high salinity (Esmaili et al. 2008). Grattan and Grieve (1992) argued that "When salinity and nutrient deficiency are both factors limiting growth, relief of the most limiting factor will promote growth more than the relief of the less limiting factor." But one point is certain that nitrogen metabolism is of central importance under salt stress.

Rice is considered as a salinity sensitive crop. However, crop damage may vary with the timing of application of salt stress and the crop growth stage. Seedling and flower initiation are the most sensitive periods (Radanielson et al. 2018). Reduction in water and nutrient uptake and root permeability under high salinity concentrations have been related to the misbalanced uptake of N absorption by plant under salinity stress (Frota and Tucker, 1978). In some crops such as cotton and corn, N application increased the dry matter under high salinity (Homaee et al. 2002). In general, it is observed that the halophytes grew in highly saline and N-deficient environments and glycophytes grew in mildly saline, and N-deficient environments respond similarly to added N.

Salinity affects N metabolism at various levels. Salinity affects the uptake and reduction of N and thus protein synthesis that causes reduced plant growth rate. But, the effect of salinity on growth and metabolism varies with different N sources. Botella et al. (1997) studied the efficiency of uptake of different nitrogen sources, viz., nitrate (applied as [$Ca(NO_3)_2$]), ammonium (applied as ammonium sulfate [$(NH_4)_2SO_4$]), or a mixture of both under salinity stress in wheat (*Triticum aestivum* L.). In general, the salinity reduced shoot and root growth. They concluded that under saline conditions or periods of low irradiance, a mixture of NO_3 and NH_4 is best suited. Earlier, the group (Botella et al. 1993) reported that salinity decreases nitrate reductase activity in wheat plants and kinetic parameters of NO_3 uptake are affected more than those of NH_4 uptake, thus affecting NO_3 more than NH_4. Later, Grattan and Grieve (1999) reviewed that the form in which N is applied, i.e., NH_4^+ or NO_3^- to plants under salt stress, is important. Generally, plants such as wheat, maize, and melon showed more salt sensitivity when NO_3^- was used as a N source. Ullrich (2002) suggested that higher concentrations of Na^+, K^+, and Mg^{2+} inhibit NO_3^- and NH_4^+ uptake and assimilation to a different extent. Among the combination of anions with these cations (i.e., Na^+, K^+, and Mg^{2+}), generally sulfate is more toxic than chloride.

The presence of Na^+ ions impairs the uptake of ammonium ions into the plant (Palfi 1965). But still, the plants have evolved strategies to maintain the homeostasis under salt stress conditions. Some of such mechanisms include ion transport and compartmentation and synthesis of compatible solutes. Many of these compatible solutes are compounds, such as amino acids, amides, and betaines (N containing) (Reddy et al. 2017). Interestingly, salinity has a pronounced effect on nitrogen metabolism in old leaves than in young leaves (Wang et al. 2013), and old leaves showed a higher concentration of NO_3^- content than young leaves. Studies in rice suggest that the upregulation of nitrate transporter gene OsNRT1;2 enhances the accumulation of NO_3^- in the old leaves (Wang et al. 2013). Xu et al. (2016) indicated that under salt stress, nitrogen metabolism not only gets enhanced but also rearranged for the synthesis of more compatible solute to cope with adverse conditions.

13.2.1.1 Salinity and Nodulation

Soil salinity also disrupts the symbiotic N_2-fixation systems in nodulating plant species, despite the optimum growth of *Rhizobium* under such conditions. Lakshmi et al. (1974) demonstrated that under saline or alkaline conditions, root system lacks root hair, mucilaginous layer, and infection thread formation in spite of optimum growth of *Rhizobium* under such conditions. Later, Tu (1981) used scanning electron microscopy to show that in soybean root surfaces, the colonization by *Rhizobium japonicum* decreased when plants were grown in the salinized culture medium. At 1.2% NaCl or higher, the nodulation was completely eliminated, and in general, an increase in salinity caused a decrease in soybean fresh weight and plant height.

Singleton and Bohlool (1984) used the split-root system and evaluated the effect of different concentrations of NaCl (i.e., 0.0, 26.6, 53.2, and 79.9 mM) on soybean. Even 26.6 mM NaCl caused significant reductions in nodule number and weight and limited the shoot nitrogen yield. Nodule number and weight decreased by ~50% at 26.6 mM, and by more than 90% at 53.2 and 79.9 mM NaCl. Singleton and Bohlool (1984) also evaluated the effect of time of salt addition on nodule formation. In half root system studies, 53.2 mM NaCl was applied at 0, 4, 12, and 96 h from inoculation. By delaying the application of salt for 12 h, an increase in nodule number, weight, and shoot N was noted. They believed that the early steps involved in nodule formation were extremely sensitive to even low concentrations of NaCl.

Sensitivity to salt is also different among different plants. Bernstein and Ogata (1966) compared the inhibitory effect of salinity and nitrate-fertilized cultures on Lee soybeans and California common alfalfa. Inoculated Lee soybeans were more sensitive to salinity than the nitrate-fertilized cultures, whereas the nodulation in California common alfalfa showed relative tolerance to salinity. However, it was observed that the decrease in growth by salinity was the same as that for nitrogen-fertilized and nitrogen-fixing cultures.

13.2.2 Interaction of Salinity with Phosphorous

Phosphorus is an essential nutrient for plants in the form of ions PO_4^{3-} and HPO_4^{2-}. It is a part of DNA molecules, which store energy (ATP and ADP). Phosphorus is most commonly found in rock formations and ocean sediments as phosphate salts and is released through weathering in soil water to be absorbed by plants. But the quantities of phosphorus (P) either inorganic phosphate (Pi) or organophosphates are generally small in soil, and it is often a limiting factor for plant growth. This is why it is often applied as phosphate fertilizers on farmland. Inorganic phosphate (Pi) strongly interacts with divalent and trivalent cations, and the organophosphates require hydrolysis to release phosphate for root uptake. Soil salinity significantly reduces P uptake because phosphate ions precipitate with Ca ions (Bano and Fatima 2009). Phosphate has a high sorption capacity to soil particles, which causes low mobility and thus reduced availability for uptake by plants (Peret et al. 2014). Also, the solubility of P is greatly reduced in salt-affected soils due to high Na concentration and soil pH, and the plants growing on such soils face the double challenge of salinity and P deficiency.

The interaction between salinity and phosphate nutrition of plants is perhaps more complex than that between salinity and N. Depending upon plants selected and conditions of the experiment, different results can be obtained. The interaction is highly dependent upon the plant species (or cultivar), plant developmental age (Zhukovskaya 1973), the composition and level of salinity, and the concentration of phosphate in the substrate. In most of the crop plants tested, the addition of P to saline soils increased crop growth and yield (Champagnol 1979). Although the effect of salinity on the nutritional status of P in plant is different from that of N, studies on interactive effects of salinity and substrate phosphate on soybean (Grattan and Mass 1985), sesame (Creda et al. 1977), corn, wheat, barley, cabbage, and broccoli (Bernstein et al. 1974) revealed leaf injury under saline and a high phosphate regime. It was interpreted as the toxicity of P which was induced by salinity. Nieman and Clark (1976) also demonstrated similar results in corn. P concentration of 2 mM caused P accumulation and toxicity under salinity. Studies carried out by Awad et al. (1990) under low P resulted in an increase in the salt tolerance of tomato plants in response to elevated P concentrations.

Kalfia et al. (2000) used radiophosphorus (^{32}P) to study the effect of high NaCl (0–120 mM) stress on the availability of inorganic phosphate (Pi 1.25 mM) in micropropagated potato (*Solanum tuberosum* L. cv. Russet Burbank) for 48 h. The ^{32}P activity of topmost trifoliate leaf was increased with time but was decreased with increased NaCl concentrations. At 48 h, increased NaCl concentration in medium showed a greater ^{32}P activity of the root tips, but less translocation of Pi into leaves was less. In the presence of 120 mM NaCl, when Pi concentration was increased from 0 to 2.5 mM, ^{32}P activity decreased in root tips but translocation into the topmost leaves occurred more efficiently. Two cultivars of barley were treated in vegetative stage under hydroponics with different concentrations of NaCl (i.e., 0, 100, 200, and 300 mM) and three levels of P (15, 30, and 55 μm L^{-1}). With increasing NaCl shoot and root length, shoot fresh and dry weight, nutrient elements (viz., K, P, Cl), soluble sugar contents, and compatible solute proline decreased. But with increased phosphorus levels, only the Na content in the shoots decreased and other parameters increased. This suggests that mineral ion accumulation for osmotic adjustment and restricted Na^+ accumulation in shoots were responsible for phosphorus enhancement of the salt tolerance of barley (Sima et al. 2012). Phosphorus/salinity interactions reported range from an induced enhancement of salinity tolerance by phosphorus to antagonism between phosphorus fertilization and salinity. Other studies report no interactions or variable interactions according to species (Gibson 1988). Gruber et al. (2013) and Kellermeier et al. (2014) compared the effect of nutrient deficiency on root architecture and revealed that low inorganic phosphate is one of the major factors that control the length of the primary root.

13.2.3 Interaction of Salinity with Potassium

Potassium is a macronutrient, constitutes ~10% plant dry weight, and the most abundant cation (Véry and Sentenac 2003). Under normal growth conditions, K^+ concentration in the cytosol is maintained at 100 mM (a constant value). Maintenance of this intracellular concentration is detrimental as K^+ is crucial for growth, development, and reproductive processes, including germination, osmoregulation, stomatal regulation, cytosolic pH regulation, phloem loading, and unloading (of sugars), and as a counterion for nitrate translocation, enzyme activation, membrane potential stabilization, and protein trafficking (Assaha et al. 2017). Since salt stress disturbs the cellular K^+ homeostatic balance (Assaha et al. 2017), maintenance of high cytosolic K^+/Na^+ is essential for salt stress tolerance (Maathuis and Amtmann 1999; Anschütz et al. 2014) and for optimal metabolic functions. Under salt stress, Na^+ competitively inhibits K^+ uptake, and Na^+ interferes with various K^+-dependent processes. For example, Na^+ replaces K^+ from binding sites of enzymes causing enzyme deactivation and altered metabolic processes (Munns and Tester 2008). The K^+ transport and availability of plants depend on exchange with other cations and its release and/or fixation with clay minerals (Bar-Tal et al. 1991).

It has been demonstrated that K^+ application ameliorates the salinity toxicity. Experiments with tomato showed that salinity decreased shoot and root dry weight and leaf area at low levels of K. But supplementation with 2 mmol K ameliorated NaCl effects and enhanced growth. However, salinity reduced net K uptake rates and K translocation from root to shoot, resulting in lower K root concentration and higher K shoot concentration. The inhibitory effect of salinity on translocation increases with low K concentrations, and the K addition results in decreases of Na uptake in the shoot (Al-Karaki 2000). Hussain and coworkers showed that application of K_2SO_4 in wheat increases yield and lessen the adverse effect of Na. It is thus a useful approach to increase crop production in saline soils. Reduced salinity damage was observed in certain crops such as wheat, sunflower, onion, beans, corn, and cotton when high concentrations of K were added to growth media (Lagerwerff and

Eagle 1962; Helal and Mengel 1979; Jeschke and Nassery 1981). Although plants show high selectivity of K^+ over Na^+, excessive amounts of K^+ may be detrimental to some plants. Potassium (K^+) has been shown as a major factor in providing resistance to salinity, drought, and fungal diseases. In general, the application of K to fields diminishes the chances of fungal, bacterial, and insect pest diseases in plants (Amtmann et al. 2008).

Accumulation of Na^+ is deleterious for plants, as it induces cytosolic K^+ efflux, which disturbs the cellular homeostasis and causes (i) oxidative stress, (ii) interference in Ca^{2+} and K^+ functions, (iii) nutrient deficiency, (iv) retarded growth, and (v) the death of plant cells. In plants, Na^+ competes with K^+ for uptake through (i) high-affinity K transporters (HKTs) and (ii) nonselective cation channels (NSCCs). Na^+ causes membrane depolarization and uptake of K+ through K^+ inward-rectifying channels (KIRs) gets difficult. This leads to activation of activating potassium outward-rectifying channels and an increased K^+ leakage from the cell. Thus, the overall effect is the influx of Na^+ that depolarizes the membranes and causes K^+ efflux. Minimizing Na^+ uptake and preventing K^+ losses help to maintain an optimum K^+/Na^+ ratio in the cytoplasm of plant cells under salt stress (Wakeel 2013).

A variety of genes encoding K^+ transporters (for high/low-affinity K^+ uptake) and channels have been identified in *Arabidopsis*. The high-affinity K^+ transporter 5 is associated with K^+ accumulation and belongs to KUP/HAK/KT families. This transporter is located in primary and lateral roots of epidermal cells, and, therefore, in salt-affected soils, an increase in the concentration of K^+ causes HKTs and NCCSs to be responsible for enhanced K^+ uptake and reduce Na^+ influx (Wakeel 2013; Ghosh et al. 2016).

Studies in molecular genetics and plant electrophysiology suggest that the ability of a plant to maintain a high cytosolic K^+/Na^+ ratio appears to be critical to plant salt tolerance (Shabala and Cuin 2008). HKT2;1 from other monocots, including wheat (*T. aestivum*, TaHKT2;1), barley (*Hordeum vulgare*, HvHKT2;1), and reed (*Phragmites australis*, PhaHKT2;1), is K^+-permeable and is vital in stress tolerance. The high-affinity K^+ transporter, that is, HKTs, is a family transporter of two types: (i) class I specific for Na^+ and (ii) class II specific for Na^+ and K^+ (Garciadeblás et al. 2003). The difference between the two classes (i.e., class I and II) lies in the polypeptide of the selectivity pore-forming motif. For class II members found in monocots, it is GGGG, and for class I members found in both monocots and dicots, it is SGGG (Platten et al. 2009; Deinlein et al. 2014). It is well documented that high concentrations of Na^+ compete with K^+ uptake (Botella et al. 1997) but external K^+ levels are low as the specificity for uptake increases. Interestingly, at higher K^+ concentration (>0.5 mmol L^{-1}), Na^+ competitively inhibits K^+ influx (Botella et al. 1997). Contrastingly, Bar-Tal et al. (1991) demonstrated in corn that increased salinity did not reduce K concentration in the dry matter; and K fertilization did not eliminate the deleterious effects of salinity on crop yield, despite the increase in K content of the plant and reduced Na:K ratio in the plant tissue.

13.3 Effect of Salinity on the Soil Microbes

The main three targets for achieving a sustainable planet are sustainable water security, food security, and sustaining biodiversity and ecosystem services that are responsible for the stable functioning of the earth systems. These targets have a direct connection with soil biochemistry that, in turn, is being regulated by the soil microbial community. Soil microbes play various vital roles in the functioning of terrestrial ecosystems, but still little has been discovered so far. This major fragmented and incomplete gap in a mechanistic understanding is particularly true in case of soils having high a concentration of salts. The area of land affected by salt exposure is increasing with each passing day.

Soil salinization has direct impacts on plants and also causes several structural and functional changes in microbes such as on biomass, respiration, growth, and carbon utilization efficiencies (Rath and Rousk 2015). But the mechanistic understanding behind its effects on soil microorganisms is lesser known.

13.3.1 Microbial Biomass

With the increasing saline conditions, plant growth becomes sparse, thereby reducing the input of organic matter, and hence, microbial biomass is often found to be low. However, the percentage of microbial biomass of the total SOM sometimes decreases in saline soils, indicating a direct negative impact on biomass (Rietz and Haynes 2003; Sardinha et al. 2003). Rietz and Haynes (2003) studied the effects of irrigation-induced salinity on the size and activity of microbial biomass in vertic soils on a Zimbabwean sugar estate. They concluded that a significant negative exponential relationship exists between electrical conductivity (EC), microbial biomass carbon (MBC), percentage of the organic carbon present as MBC, rates of arginine ammonification, fluorescein diacetate hydrolysis, and the activities of exocellular enzymes such as β-glucosidase, alkaline phosphatase, and arylsulphatase. But interestingly with the increase in salinity, the metabolic quotient, that is, respiration-to-biomass ratio or qCO_2 increased, thus indicating that increased salinity and sodicity leads to progressively smaller, stressed, and less metabolically efficient microbial community. EC is used as the salinity level to establish discernable systematic relationships with microbial biomass-C (expressed per gram SOC). However, to date except for Australian soils, this relationship shows lack of observable systematic trends between estimated EC and soil microbial biomass for other soil types (Rath and Rousk 2015).

Similarly, Wichern et al. (2006) demonstrated that with increasing salinity, the rate of microbial-assisted decomposition of maize gets decreased leading to the recovery of the increased amount of maize-derived particulate organic matter. In addition to this inorganic nitrogen, mostly NH_4^+ form also increases with salinity due to inhibition in nitrification (Swarup 1994).

13.3.2 Microbial Respiration

Soil microbial respiration is one of the most studied parameters describing the response of the microbial activity to salinity. It gives a clear measure of the total microbial contribution to C cycling. It has been observed that with increase in salinity, there is a consistent decline in the rate of microbial respiration and decomposition of the organic matter. Since soil carbon is the primary determinant of soil microbial community, therefore, lower SOM leads to lower availability of C ultimately causing lower respiration rate (Garcia and Hernandez 1996).

Nelson et al. (1996) and Saviozzi et al. (2011) through their different studies have concluded that the types of salts used during experiments (e.g., sodic Na^+ salts vs. Ca^{2+} salts) have different impacts on the rate of respiration. While the saline conditions decline the rate of respiration, the sodicity leads to increase in the same. A probable mechanism to better explain this increase in respiration is that sodicity causes the dispersion of soil aggregates and higher availability of organic substances.

13.3.3 Microbial Growth and C-Use Efficiency

The information on the rate of microbial biomass production is rare in the case of terrestrial environments. Most of the studies have been conducted in aquatic systems for determining microbial biomass by using ^{3}H-labeled leucine and thymidine. These studies have shown that with the increase in salinity, the microbial biomass decreases (Pedrós-Alió et al. 2000; Gasol et al. 2004). Similarly, in an in situ study, Rousk et al. (2011) have found that high salt concentrations could decline the microbial growth by more than 90%. Likewise, the lacuna regarding soil microbial C budget is yet to be filled. Microbial anabolic and catabolic use of carbon ultimately leads to the development of long-term C stock. Initially, plants act as the source of C that forms SOM but later most of the SOM results from microbes rather than plant-derived C. The fraction of microbial C that is allocated to anabolic processes (i.e., growth) rather than catabolic processes contributes to SOM stocks (Kleber 2010; Malik and Gleixner 2013). In the future, further active research involving the comparative analysis of anabolic-to-catabolic processes is to be conducted to understand the microbial C dynamics.

13.3.4 Microbial Enzyme Activities

The extracellular enzyme activity is reported to be lower in naturally saline soils than non-saline soils. The probable mechanisms used to explain these results are that an increase in salinity has direct negative impacts on organic matter and microbial biomass content, thereby affecting the enzyme activity. Results of Batra and

Manna (2009) showed that osmotic stress in saline conditions reduced both the dehydrogenase enzyme activity and MBC, whereas these parameters showed a positive relation with the organic content of the soil. To further our understanding of decrease in enzymatic activities, another mechanism that has been proposed so far is with low osmotic potentials, microbial communities allocate less resource to protein production and release fewer proteins into the surrounding medium. Besides, this increase in salinity leads to denaturation of proteins, reducing their solubility and thus resulting in lower enzymatic activity. However, the results may show variations depending on the difference in the soils and enzymes (Frankenberger and Bingham 1982).

13.3.5 Fungal-to-Bacterial Balance and Microbial Community Structure

Earlier studies have shown a decrease in the fungal-to-bacterial ratio in the salt-affected soil (Sardinha et al. 2003; Pankhurst et al. 2001). However, during in situ incubation experiments with different saline treatments on naturally saline soil and non-saline soil, an increase in ergosterol-to-microbial biomass ratio was observed (Wichern et al. 2006). But incubating the soil samples with added organic matter at different salinities leads to a reduction in the proportion of fungal phospholipid fatty acids (Chowdhury et al. 2011). Although so far information on the impact of soil salinity gradients on fungi and archea is very rudimentary, yet it has a deep impact on shaping microbial communities. Fungi are more sensitive toward salinity stress than bacteria and this difference in salinity tolerance causes a major shift in the microbial community in saline soil versus non-saline soil. As a shift in archeal community, composition along a soil salinity gradient and fungal composition along a marshland salinity gradient have already been observed (Walsh et al. 2005; Mohamed and Martiny 2011). Molecular characterization of soil microbial communities under soil salinity has yet to be deciphered.

13.3.6 Microbial Tolerance Assessments

Preexposed bacterial populations are found to be salt tolerant on the level of bacterial strains in culture. At the community level, microbial communities from a saline soil have salt adaptation. Some factors other than salinity tolerance also have roles in shaping community structure. Soil microbial respiration showed no relationship between soil salt concentration and tolerance (Rousk et al. 2011; Asghar et al. 2012; Yan and Marschner 2012).

13.3.7 Microbial Resistance and Resilience

Like other fields, more extensive research has been conducted in aquatic systems rather than in terrestrial systems. However, certain studies have been conducted to observe the effect of changing salinity on soil microorganisms. Microbial communities exposed to high salt concentration exhibit a high degree of resilience. After amelioration of natural saline soil, the thriving microbes appeared to recover both biomass and respiration (Yan and Marschner 2012).

13.3.8 Osmoadaptation Mechanisms

Salt stress is primarily osmotic stress and is a major threat to soil microbial communities which in turn alters various processes such as organic matter turnover, ecosystem biogeochemical cycling, and releasing inorganic plant nutrients as nitrate (through nitrification), sulfate (through sulfur oxidation), and phosphate (through phosphorus mineralization) (Marschner 1995; Raich and Potter 1995; Setia et al. 2012; Yan et al. 2015). In order to combat this stress, microbes have developed different mechanistic approaches. The halophilic/halotolerant microbes have evolved two varied osmoregulatory mechanisms, the KCl-type and other the compatible-solute type. The highly halophilic archaea of the family Halobacteriaceae that include genera like *Halobacterium*, *Haloarcula*, *Haloquadratum*, *Halorhabdus*, *Natronobacterium*, and *Natronococcus* belonging to order Haloanaerobiales and bacterium such as *Salinibacter ruber* have K^+ accumulation strategy. Intracellular K^+ cation contributes to the maintenance of both the osmotic balance across the membrane and in stabilizing the turgor pressure (Empadinhas and da Costa 2008).

HPLC and NMR studies have shown a range of highly diverse eubacterial compatible solutes. The major compatible solutes are either amino acids such as proline (a proteinogenic amino acid) or its derivatives like betanines, ectoines, N-acetylated diamino acids, and N-derivatized carboxamides of glutamine or carbohydrate or its derivatives like trehalose and sucrose (Galinski and Truper 1994; Kempf and Bremer 1998). These compatible solutes get accumulated either by uptake from the surrounding medium or by de-novo synthesis. These compatible solutes serve two different functions in osmoregulating microbial cells. First, they lower the cytosolic osmotic potential and thus restore and maintain cell turgor. Second, solutes as glycine, betaine, and proline promote cytoplasmic volume and free water content at high osmolarity, thereby facilitating cell proliferation under adverse conditions. These solutes also act as the stabilizers of proteins and other cell components against the denaturing effects of ionic strength. Though the suggested mechanism behind this property is not fully deciphered, yet it is believed that osmoprotectants are kept away from the immediate vicinity of proteins and hence keeping protein surface hydrated (Kempf and Bremer 1998). Some of these solutes are common in nature while others are reported to be present exclusive in specific groups of organisms. Under saline conditions, accumulation of diglycerol phosphate has been identified in members of the genus *Archaeoglobus*. Strains of *Thermus thermophiles* depending on their salt tolerance can be divided into three groups and are synthesizing either trehalose (~1% NaCl) or mannosylglycerate (~3% NaCl) or both (5–6% NaCl) as their compatible solutes (Empadinhas and da Costa 2008).

13.4 Effect of Salinity on Plant Health

In general, all soils contain salts; however, many salts such as nitrates and potassium are essential for plants (Kotuby et al. 2002). On the basis of plant growth responses to saline conditions, they are divided into two groups: halophytes (salt-loving) are capable of completing life cycle in the salt concentrations above 300 mM and the other group glycophytes (sugar lovers) and cannot survive in salt conditions (Flowers et al. 1977). Although halophytes do not show any unique metabolic differences as compared to glycophytes (Flowers et al. 1977; Niu et al. 1995; Nelson et al. 1998), instead they have the ability for osmotic adjustments via internal compartmentation that keeps toxicons away from the cytoplasm through the energy-dependent transport into the vacuole (Apse et al. 1999; Binzel et al. 1988). Some halophytes exclude Na^+ and Cl^- through glands and bladders (Hasegawa et al. 2000). The ability of halophytes to tolerate salt shock is the capacity that allows them to establish and achieve a metabolic state for growth in the saline environment (Braun et al. 1986, Cushman et al. 1990). Plants differ greatly in their tolerance to salinity. Numerous studies are performed to study salt tolerance in seedlings of tree, for example, some of the studies include *Phoenix dactylifera* L. (Yaish and Kumar 2015), Yu et al. (2016) in *Arabidopsis*, Zrig et al. (2016) in sweet almond, Raga et al. (2016) in citrus rootstocks *Cleopatra mandarin* and trifoliate orange, Martins et al. (2017) in tobacco plant, Bidalia et al. (2017) in *Mitragyna parvifolia*, etc.

13.4.1 Mechanism of Salt Tolerance in Plants

Salinity tolerance among species is controlled by several genes controlling them that further depend strongly with the environmental conditions. Thus, genetic variation can only be demonstrated indirectly, by measuring the responses of different genotypes (Carillo et al. 2011). In fact, moderate salinity levels are considered best to study salt tolerance and the best suitable response parameters are growth and yield (Allen et al. 1994; Murillo-Amador et al. 2015). Tolerance can be assessed by other parameters like comparing the change in biomass production in control plants against saline-treated plants over a period of time, which normally correlates with the yield also and another aspect is looking at the survival but not for annual species (Munns, 2002; Negrão et al. 2017). Moreover, Munns and Tester (2008) explained that salinity in plants can be studied at three different levels such as a change in ionic balance (Na^+ exclusion), solute concentration around a cell (osmotic), and ability of the tissue to tolerate stress specifically by accumulating Na^+ and Cl^-. During these processes, the ability of the plant to grow under Na^+ is maintained, increased ability to produce new leaves and increased survival of older leaves, production of compatible solutes, etc., although the mechanism is not known for osmotic tolerance (Munns and Tester 2008).

13.4.2 Osmotic Adjustment and Tissue Tolerance

When plants are exposed to saline condition, one of the challenges is to adapt to a system that allows cellular sodium to be used for an osmotic adjustment (Waisel 1972). Osmotic tolerance is a very important feature to prevent water loss in plant cells under salinity that causes negative osmotic potential. It helps the plant to overcome the physiological drought, imposed due to salinity stress, and also helps to maintain stomatal conductance and leaf expansion (Rajendran et al. 2009). Reduced rate of growth and stomatal conductance are one of the results of the osmotic effect caused during salinity, irrespective of the plant tolerance capability (Fricke et al. 2004; James et al. 2002). But if the accumulation of salt exceeds toxic concentrations, senescence of older leaves occurs and the formation of new leaves is not supported by the photosynthates. The increase in osmotic tolerance results in increased leaf area and helps only those plants with sufficient water supply (Munns and Tester 2008). Furthermore, in plants, the salt uptake is restricted by the synthesis of compatible solutes to adjust their osmotic pressure under salt stress. The tolerance of tissue involves the survival of older leaves. This requires the synthesis and accumulation of compatible solutes in the leaf and compartmentalization of Na^+ and Cl^- at the cellular and intracellular level (Munns and Tester 2008). Compatible solutes are nontoxic, low-molecular weight, and highly soluble compounds, which play a role in plant osmotolerance (Ashraf and Foolad 2007). These compatible solutes include sucrose, polyols, proline, trehalose, and quaternary ammonium compounds including proline betaine, glycine betaine, hydroxyproline betaine, choline *O*-sulfate, alanine betaine, and pipecolate betaine. In plants, these metabolites are connected with major fluxes such as carbon and nitrogen under saline conditions. In addition to that, these osmolytes stabilize subcellular structures, free radical scavengers, buffer cellular redox potential, and storage of sinks for carbon and nitrogen during stress, being hydrophilic, able to replace water at the surface of proteins or membranes (Hasegawa et al. 2000; Chen and Murata 2002). A large number of stress proteins are also induced due to osmotic stress that provides dehydration tolerance to plants, for example, osmotins, dehydrins, and late-embryogenesis-abundant proteins, heat shock proteins, and chaperons (Bray 1997; Chinnusamy et al. 2005; Zhang et al. 2008; Riadh et al. 2010).

13.4.3 Ion Homeostasis

During salinity, ion-specific stress is caused that alters the K^+/Na^+ ratios and leads to build up Na^+ and Cl^- concentrations that are injurious to plants. The ion influx and efflux at the plasma membrane and tonoplast, specifically Na^+ uptake and vacuolar compartmentation, are highly important in terms of salinity adaptations in plants (Tuteja 2007). The maintenance of high cytosolic K^+/Na^+ ratio is essential for plant to grow under saline conditions; however, plants use strategies like vacuolar compartmentation of Na^+ ions, extrusion of Na^+ ions out of cell, and diminishing Na^+ entry to cells, however at high salt sodium chloride (NaCl) salt concentrations where ion exclusion does not work (Yamaguchi and Blumwald 2005). It has been observed that most of the studies focused on the Na^+ exclusion and control in the plants growing under saline conditions because under such conditions it has been found that in the majority of plants, the toxic concentrations of Na^+ reach earlier than Cl^- (Munns and Tester 2008). Therefore, the tolerance mechanism involves the ability of plants to reduce ionic stress by minimizing $[Na^+]$ in cytosol, particularly in transpiring leaves. During the process, up- and downregulation of the expression of ion channels and transporters take place that controls Na^+ in plants (Munns and Tester 2008; Rajendran et al. 2009). These include transport proteins such as H^+-translocating ATPases pumps, antiporters/symporters carriers, and non-selective cation channels that regulate ion fluxes across plasma membrane and tonoplast (Tuteja 2007). In leaves, Na^+ exclusion is mainly due to low net Na^+ uptake by roots and tight control of net loading in the stele while roots ensure that Na^+ should not accumulate to toxic concentrations within leaf blades (Davenport et al. 2005). However, failing to ensure Na^+ exclusion after a certain time leads to the premature death of older leaves due to toxicity depending upon the species (Munns and Tester 2008). In plants, the demand for organic solutes increased if Na^+ exclusion is not compensated for by the uptake of K^+. Synthesis of organic solutes further disturbs plant energy balance. However, membrane receptor helps to sense the extracellular Na^+ while membrane proteins and Na^+ sensitive enzymes sense intracellular Na^+ (Munns and Tester 2008).

13.4.4 Physiological and Metabolic Adjustment

The most important metabolic processes in a plant cell are photosynthesis and respiration. Generally, a decrease in stomatal aperture can be observed under salinity but not necessarily the rate of photosynthesis per unit leaf area changes (Munns and Tester 2008; Negrão et al. 2017). In terms of evolutionary adaptations, in *Mesembryanthemum crystallinum* (Niewiadomska et al. 2004) in *Atriplex lentiformis* (Zhu and Meinzer 1999), photosynthetic metabolism shifted from C_3 to CAM and C_4, respectively, under salinity to achieve higher water use efficiency. A large stomatal conductance decrease is observed under many species such as durum wheat genotypes, rice plants, etc. (Moradi and Ismail 2007; James et al. 2002). Many studies reported that salinity did not affect the photosystem II (PSII) in the tolerant species, for example, wheat (James et al. 2002). Upon stomatal closure, the

CO_2 also decreases in the cells and consequently decreases the Rubisco activity, thus limiting carboxylation (Chaves et al. 2009). However, the salt-tolerant species such as *Eutrema salsugineum* is able to maintain intercellular CO_2 concentration (C_i) (Stepien and Johnson 2009). The amount of chloroplast density per unit leaf area increases due to changes in leaf anatomy and leaf expansion that leads to decreased photosynthesis measured on a unit basis (Munns and Tester 2008). Under salinity, the electron trapping in PSII becomes inefficient due to dissociation of LHC II and PSII (Havaux 1993). In a number of species, for example, barley, tobacco, goosefoot, etc., a decrease in maximum quantum yield and increased non-photochemical quenching have been recorded (Kalaji et al. 2016). While in tomatoes and cucumber seedlings the efficiency of PSII open reaction centers in light, PSII efficiency in light and electron transport chain efficiency are reduced (He et al. 2009; Zhang and Sharkey 2009). Furthermore, the donor side of PSII is found to be more affected than the acceptor side in wheat (Mehta et al. 2010). The photosynthetic tolerance in plants is brought by a range of adaptations at different scales such as morphological-to-biochemical adaptations. The major adaptation under salinity stress is to minimize water loss and maintaining carbon gain in plants (Popova et al. 1995). However, an increase in plants respiration is also observed under stress, which is attributed to energy costs for acclimation (Larcher 1995). Increased respiratory oxygen uptake is also observed in plants upon exposure to high salt concentrations (Takemura et al. 2000). These increased respiratory rates enhance the generation of reactive oxygen species (ROS) that causes mitochondrial damage, whereas ROS formation is minimized by an alternative pathway, the alternative oxidase in plants under stress conditions (Purvis and Shewfelt 1993; Rhoads et al. 2006).

13.4.5 Plant–Pathogen Interaction Under Salinity

Plant–pathogen interaction is a two-way communication system in which both the plant and the pathogen have evolved a suite of genes that enables the interaction (Boyd et al. 2013). Pathogens attack plants because during their evolutionary development, they have acquired the ability to live off the substances manufactured by the host plants, and some of the pathogens depend on these substances for survival. Simultaneously, plants have developed a variety of defense mechanisms against the pathogen attack such as resistance (i.e., ability to check pathogen population) and tolerance (i.e., ability to mitigate the negative effects of the pathogen) (De Gara et al. 2003). However, this interaction is dramatically altered by the abiotic stresses that are further dependent on the patho-system and stress intensity (Bostock et al. 2014). The development of diseases also depends on the influence of the surroundings on the host's genetic responses in the presence of a pathogen and its metabolites such as nongenetic factors, acting before infection; consequently, affecting the host susceptibility to diseases is called predisposition (Schoeneweiss 1975). Presence of abiotic stress can induce or arrest the infection ability of some pathogens causing severe diseases (Pandey et al. 2015). Table 13.1 is an attempt to summarize the same.

Table 13.1 List of plants and the pathogens affected by salinity

Plant	Pathogen	Observation	References
Gossypium spp.	*Aspergillus* sp. *Penicillium* sp.	Able to grow in the presence of 20% or more of NaCl in the growth medium	Tresner and Hayes (1971)
Agrostis palustris	*Phytophthora* spp.	Out of four isolates, three were capable of forming sporangia and releasing zoospores at ECe ≥ 4.0 dS/m, while *P. parasitica* were able to release spores at ECe ≥ 8–10 dS/m	Blaker and MacDonald (1985)
Chrysanthemum sp.	*Phytophthora cryptogea*	Disease severity increased when pathogen-inoculated plants were exposed to salinity stress at 4 h or 12 h, but no affect after 24 h and 48 h	MacDonald (1984)
Citrus	*Phytophthora parasitica*	Root rot of citrus was more severe in the presence of salinity, because of increased tissue severity and/or inhibition of root growth and regeneration	Blaker and MacDonald (1986)
Agrostis palustris	*Pythium aphanidermatum*	An increase in the mycelial growth and zoospore production was observed up to 7.1 ds/m, while zoospore production was completely inhibited at 14.2 ds/m	Rasmussen and Stanghellini (1988)
Gossypium spp.	*Fusarium oxysporum* f. sp. *Vasinfectum*	The viability of chlamydospore and germ tube length increased in saline medium (10 ds/m)	Ragazzi and Vecchio (1992)
Solanum tuberosum	*Verticillium dahlia*, *Alternaria solani*	In the presence of salt, the disease symptoms such as height and maturity increased	Nachmias et al. (1993)
Cyclamen persicum	*Fusarium oxysporum* f. sp. *Vasinfectum*	The disease suppression was marginal, while addition of NaCl at 0.25 to 0.50 g/l of potting mix had growth benefits	Elmer (2002)
Cotton	*Fusarium oxysporum* f. sp. *Vasinfectum*	The severity of disease increased with increase in nutrient solution of EC 20 md/cm compared with the nonsaline solution	Turco et al. (2002)
Asparagus sp.	*Fusarium oxysporum* and *F. proliferatum*	NaCl treatment suppressed the growth of *Fusarium* crown and root rot of *asparagus*	Elmer (2003)
Olive	*Verticillium dahliae*	Saline irrigation probably exacerbates disease expression in a 3-year study on olive, a susceptible host of *V. dahlia*	Levin et al. (2003)

(continued)

Table 13.1 (continued)

Plant	Pathogen	Observation	References
Chili pepper	*Phytophthora capsici*	Salinity increases the mycelium growth, but with a decrease in the sporangium formation and zoospore production	Sanogo (2004)
Lycopersicon esculentum	*Fusarium oxysporum* f. sp. *lycopersici* (FOL)	The mycelial growth of the pathogen was not significantly affected under salt treatment (0, 2, 4, 6, 8, and 10 g/l), while the disease severity was enhanced with the increased salinity	Daami-Remadi et al. (2009)
Sorghum bicolor	*Macrophomina phaseolina*	Shoot and root colonization of *M. phaseolina* increased by increasing the salinity levels up to 1400 mg of NaCl kg^{-1} soil	Goudarzi et al. (2011)
Glycine max	*Penicillium minioluteum*	*P. minioluteum* ameliorated the adverse effects of abiotic salinity stress and rescued soybean plant growth by influencing biosynthesis of the plant's hormones and flavonoids	Khan et al. (2011)

13.5 Strategies to Amelioration Soil Salinity

The strategies for soil salinity reclamation and amelioration should be based on the proper understanding of the responsible factors creating saline or saline-alkali soil (Garg and Gupta 2011). Any reclamation technique is successful only when salts are entirely removed from the root zone and this can be achieved by the process known as leaching (addition of an excess amount of water to the soil surface so that salts can be pushed downward through the soil profile along with water). Other factors that can affect reclamation process include irrigation practices (as it can increase water logging conditions), drainage systems (like surface and subsurface drainage is also important as it leads to the waterlogged conditions), crop selection, etc. (Garg and Gupta 2011). With the advancement in science and technology, extensive research focuses on the methods to lower the impacts of salinity all over the world (Frankenberger and Bingham 1982). Extensive research has been done to understand the physicochemical nature of saline and sodic soils, and their amelioration in relation to soil structure and vegetation. In a 12-week study, Wong et al. (2009) observed that addition of gypsum (10 t ha^{-1}) and organic matter (10 t ha^{-1}) on the saline-sodic soil increased the growth of the soil microbial biomass, whereas the use of nitric oxide (NO) in the form of its donor *S*-nitroso-*N*-acetylpenicillamine (50 mM) protected the chickpea plants (*Cicer arietinum* L.) against oxidative stress induced by saline conditions (50 and 100 mM NaCl) by improving the biosyntheses of antioxidant enzymes such as superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase, and glutathione reductase (Ahmad et al. 2016). In a recent study, plant growth promoting (PGP) properties of halophilic and halotolerant bacteria were observed in Iğdır and Erzincan provinces (Orhan 2016). Another study by Yaish and Kumar (2015) on *P. dactylifera* L. revealed that strains PD-R6 (*Paenibacillus xylanexedens*) and PD-P6 (*Enterobacter cloacae*) possess the potential to enhance the growth and development of date palm trees under salt-stressed conditions (100 mM). Likewise, pea plants (*Pisum sativum* L. cv. Alderman) inoculated with the ACC-deaminase containing rhizobacterium *Variovorax paradoxus* 5C-2 increased total biomass of its host plants by 25% and 54%, respectively, when grown under salt stress (70 and 130 mM NaCl), and bacterial inoculation improved water relations, ion homeostasis, and photosynthesis of pea plants exposed to salt stress (Wang et al. 2013). Forni et al. (2017) reviewed that many PGP bacteria have been shown to accelerate the production of the metabolites as betaine, proline, and trehalose along with the synthesis of enzymes, like SOD and CAT, that can downregulate the oxidative damage caused by ROS in plants. In addition to these studies, Jha and Subramanian (2016) recommended the extensive application of biofertilizers, especially KSM (a potassium-solubilizing microorganism), PGP bacterium to enhance the plant growth. KSM such as *Bacillus* spp. and *Pseudomonas* spp. help plant growth by promoting solubilization of insoluble minerals (K and P), resource acquisition (macro and micronutrients), phytohormones production and by secreting different regulatory chemicals within the rhizosphere of the plant root. Plants inoculated with KSM show tolerance toward salt stress (2.3–3.5 dS m^{-1}) and low availability of P and K by decreasing lipid peroxidation and increasing their growth-related physiology.

13.6 Conclusion and Future Prospects

Soil salinity is a major global threat as it greatly influences the agricultural production and ecosystems by reducing plant growth and microbial functioning. To satisfy the increasing food demand, it is imperative to incorporate various aspects of microbial biotechnology and other nonrenewable resources (organic matter) to attain sustainable agriculture, lessen salt stress, and ameliorate salt stressed soils. In terrestrial conditions, the status of salinity is highly variable and changes with time and space. Nutritional disorder in the salt-affected soils significantly affects the plants by affecting the nutrient availability and competitive nutrient uptake from the soil. In the current omics world, developing tolerant varieties with a higher yield is an ambition of the plant biologist by using various approaches adopted by the plants to overcome harsh environmental conditions. Likewise, soil biota can cope up with increasing salinity by synthesizing and accumulating compatible solutes that involve the expenditure of energy. Therefore, routine addition of C sources like that of manures and plant residues can prove helpful in amelioration of saline soils. Employing living organisms in saline soils has been proposed for bioremediation of soil salinity and biofertilizers for stressful environments. Research is needed to be conducted to observe the effects of fluctuating salinity on soil biota. Further, understanding the origin of salts in the soil and then employing various techniques and methods (such as the addition of gypsum, leaching, irrigation methods, afforestation, etc.) of amelioration, reclamation, and management can help to build a strategy to overcome saline soil conditions. Therefore, future research lies in the holistic approach to understand the saline soil and their effect and management practices.

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