# **Chapter 11 Halophilic Microbes from Plant Growing Under the Hypersaline Habitats and Their Application for Plant Growth and Mitigation of Salt Stress**



## **Enespa, Jai Prakash and Prem Chandra**

**Abstract** Salinity of the agriculture soil is the serious issue all over the world, and it is also an important environmental factor for reduction of growth and yield of agricultural crops. The density of more salt available in soil may alter the physiological and metabolic activities in the agricultural crops and reduce the growth and production of crops both qualitative and quantitative ways. For combating against soil salinity, many transgenic salt-tolerant crops have been developed but far too little is success. For solution, in the soils the use of plant growth-promoting rhizobacteria (PGPR) can reduce soil salinity, load of chemical fertilizers, and pesticide in the agricultural field, and improve soil health, seed germination, crop growth, and productivity under saline condition PGPR accepted as potential microbes that can tolerate various atmospheric circumstances like more temperature, pH, and saline soils. In the saline environment, many halophilic/halotolerant bacteria and plants/halophytes are observed/adapted and perform a significant role in saline soil ecosystem. Innumerable microfloral communities and halophytes contain salt-tolerant gene, and they perform as an essential protagonist in subsistence for extreme environmental condition especially salt. It can be concluded that PGPR can be used as a supportable, manageable, sustainable, and economical tool for salinity tolerance and productivity of crops/plants.

**Keywords** Halophile · Hypersaline habitats · PGPR · Soil salinity · Sustainable agriculture · Salt mitigation

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A. N. Yadav et al. (eds.), *Plant Microbiomes for Sustainable Agriculture*, Sustainable Development and Biodiversity 25, [https://doi.org/10.1007/978-3-030-38453-1\\_11](https://doi.org/10.1007/978-3-030-38453-1_11)

## **11.1 Introduction**

The population of human will be expected to reach 9.8 billion until 2050 (Magallon and Dinneny [2019\)](#page-25-0). In addition, the demand for food also be increased with the enhancing population, but this demand cannot be fulfilled without soil fertility, beneficial microorganisms, and essential nutrients of the soil (Poeplau et al. [2019;](#page-27-0) Chandra and Enespa [2017\)](#page-21-0). Currently, many chemical fertilizers and pesticides are used in the soil for production of food; however, these ingredients can be increased for crop growth and productivity (Chandra and Enespa [2017\)](#page-21-0), but simultaneously it increases soil salinity and also reduces soil fertility and beneficial microorganisms present in the soils (Rashid et al. [2016;](#page-27-1) Yang et al. [2019\)](#page-31-0). The salinity in soil ecosystem is a major agrochemical/abiotic stress problem mainly in the semi-barren and waterless areas (Gu et al. [2016\)](#page-23-0). Approximately, 65% of crop's productivity is adversely affected by saline soil (Machado and Serralheiro [2017\)](#page-25-1).

A significant role is played by microorganisms in the improvement of productive soil and crop production and yield. In addition, some ions (e.g., sodium (Na+) and potassium  $(K^+)$ ) also affect the growth of plant and microorganisms and ultimately increase the soil salinity (Yan et al. [2015\)](#page-31-1). Besides these, the climate changes such as drought, shortage of water, low rainfall, and abrupt changes in temperature also increase the soil salinity (Chandra and Enespa [2016\)](#page-21-1). Reactive oxygen species (ROS), hydrogen peroxide (H2O2), superoxide (O2), hydroxyl radicals (OH**−**), lipid peroxidation, and the integrity of the membrane are other parameters of soil salinity which are produced by the cellular response (Choudhury et al. [2017;](#page-21-2) Chakraborty et al. [2018;](#page-21-3) Singh et al. [2018\)](#page-28-0). In the presence of soil salinity, organic matter, essential nutrients, and beneficial microorganisms are reduced and ultimately it negatively affects the crop's productivity (Egamberdieva et al. [2017\)](#page-22-0). Soil salinity reduces the root and shoots growth and finally decreases the crop's productivity (Glick [2014\)](#page-23-1). For the management of soil salinity, plants used various types of mechanisms (Schmidt et al. [2018\)](#page-28-1). Among all mechanisms, osmolyte is a common mechanism used by the plant. Osmolytes provide protection to the plant cell organelles and also build up compatible solutes (Chakraborty et al. [2018;](#page-21-3) El-Esawi et al. [2019\)](#page-22-1). Besides, the formation of free radicals stabilizes DNA, stress protein, and prolines during salt stress condition are other factors for survival and growth of the plant (Teh et al. [2016;](#page-29-0) Chandra and Enespa [2016\)](#page-21-1). Moreover, antioxidant enzymes such as peroxidases (POX), superoxide dismutase (SOD), and catalase (CAT) also protect against salinity and toxicity (Joseph and Jini [2010;](#page-24-0) Caverzan et al. [2016\)](#page-21-4).

However, these mechanisms are not good for a long time in the reduction of soil salinity; currently, it needs a viable method for reduction of soil salinity and improves the soil fertility and increases microbial population, plant growth, and yield at high saline condition (Ladeiro [2012;](#page-25-2) Shrivastava and Kumar [2015\)](#page-28-2). Microorganisms play a significant role in the improvement of soil fertility, crop's growth, and yield (Yan et al. [2015;](#page-31-1) Biswas and Paul [2017\)](#page-21-5). Among all microbial group, plant growth-promoting rhizobacteria (PGPR) is an eco-friendly method for plant growth

and sustainable agriculture by various ways such as the production of phytohormones, solubilization of minerals such as potassium, zinc, phosphate, and chelation of iron under saline condition (Verma et al. [2015;](#page-29-1) Yadav et al. [2015a,](#page-30-0) [b,](#page-30-1) [c;](#page-30-2) Habib et al. [2016;](#page-23-2) Ilangumaran and Smith [2017;](#page-23-3) Numan et al. [2018\)](#page-26-0). This chapter describes the role of PGPR in the improvement of soil fertility and reduction of soil salinity and crop's yield under saline condition. In addition, how halotolerant microbes and plants survive under saline condition has been also explained.

# **11.2 Halophiles, Classification, and Hypersaline Environments**

Those microorganisms can propagate and maintain their spore cycle at more saline concentrations ( $\geq$ 150 g L<sup>-1</sup>/15%) known as halophile (Ollivier et al. [1994;](#page-26-1) Oren [2008\)](#page-27-2). The halophile is categorized into three dissimilar groups on the beginning of different salt concentrations: 1) less  $(1-6\%$  NaCl), temperate  $(7-15\%)$ , and more salt concentrated halophile (15–30%) (de Lourdes Moreno et al. [2013;](#page-22-2) Chandra and Singh [2014;](#page-21-6) Yadav et al. [2019a,](#page-30-3) [2015d\)](#page-30-4). Different concentrations of salt occur in the soil, and these are found at various depths in the soil habitats. According to Or et al. [\(2007\)](#page-27-3), salt concentration and their variability are found much more than water. In the saline environment, different plants are growing known as halotolerant (halophytes) at different concentrations of salts and recorded well adaptability and perform a key character in the biogeochemical cycles (Nabti et al. [2015;](#page-26-2) Etesami and Beattie [2018\)](#page-22-3). Microbes play a major character in enhancement of herb adaptation at various saline habitats (Bringel and Couée [2015;](#page-21-7) Bang et al. [2018;](#page-20-0) Yadav et al. [2019a\)](#page-30-3). However, a limited microbial diversity is found in the extreme soil habitats/hypersaline environments due to various environmental factors and high salt concentrations (Ulukanli and Digrak [2002;](#page-29-2) Chandra and Singh [2016;](#page-21-8) Yadav and Saxena [2018\)](#page-30-5). Besides soil salinity, the saline environment is mainly found in the aquatic water such as lakes, river, pond, and sea (Sánchez-Porro et al. [2003\)](#page-28-3). From saline environments, the food or food-based products, plants, and animals contain salts (Maturrano et al. [2006;](#page-26-3) Ventosa et al. [2015\)](#page-30-6).

## **11.3 Halophilic/Halotolerant Microbial Diversity in Soil**

Soil salinity affects the structure, composition of microbial species, and also bacteriological populations present in the rhizospheric regions of crops. These communities have different groups, which show modified structural and physiological properties under hypersaline condition (Bever et al. [2012;](#page-20-1) Mendes et al. [2013\)](#page-26-4). However, bacterial communities are dominant as compared to other microbial communities (e.g., virus, fungi, protozoa, and algae), and it is found in the rhizospheric region of the

plant under saline condition (Mukhtar et al. [2017;](#page-26-5) Yamamoto et al. [2018;](#page-31-2) Chandra and Enespa [2019b\)](#page-21-9). Besides rhizosphere, bacterial communities are also recorded endophytic region, in salt lakes, river water, and root nodules (Albaggar [2014;](#page-20-2) Leite et al. [2017\)](#page-25-3). But in the saline soil, bacterial communities do not define a similar group of phylogeny but signify a assemblage which has progressed in altered types of microorganisms that belong to the genera *Actinopolyspora*, *Bacillus, Halomonas Micrococcus, Marinococcus, Pseudomonas, Salinicoccus,* and *Vibrio* which are mainly found in the hypersaline region (Ventosa et al. [1998;](#page-30-7) Soto-Padilla et al. [2014;](#page-28-4) Chandra et al. [2014;](#page-21-10) Verma et al. [2017b;](#page-30-8) Yadav et al. [2018a,](#page-31-3) [b,](#page-31-4) [d\)](#page-31-5). These genera belong to both Gram-positive and Gram-negative bacteria showing rod-, comma-, and cocci-shaped cell. However, Gram-negative bacteria appear to be dominant in saline environments (Ventosa et al. [1998;](#page-30-7) Canfora et al. [2014\)](#page-21-11). In Gram-negative bacteria, root-nodulating bacteria showing root-colonizing property are considered to be a halotolerant group (Zahran [1997\)](#page-31-6). These bacteria have capable of nitrogen fixation and improve soil fertility at high concentration. A halotolerant bacterium *Swaminathania salitolerans* gen. nov., sp. nov. was isolated from the rhizosphere, roots, and stems of mangroveassociated wild rice (Loganathan and Nair [2004\)](#page-25-4). Another bacteria belonging to the genus of *Azospirillum*, *Bacillus, Enterobacter,* and *Azotobacter* were isolated from the different agricultural under saline soils (Alamri and Mostafa [2009;](#page-20-3) Fendrihan et al. [2017\)](#page-22-4). The popular nitrogen-fixing bacterium *Rhizobium* is linked with marsh grass *Spartina alterniflora* as a halotolerant plant has also been isolated and identified from hypersaline condition (Bedre et al. [2016\)](#page-20-4).

Besides, another nitrogen-fixing bacterium *Bacillus* was screened from salty soils of Egypt, and it showed acetylene reduction activity at 5% NaCl concentration (Zahran et al. [1995\)](#page-31-7). The genus *Azotobacter* is the free-living nitrogen-fixing bacterium showing a significant role in different environmental conditions such as soil, water, and sediments at the high salt concentration (Akhter et al. [2012;](#page-20-5) Sahoo et al. [2014\)](#page-28-5). *Azotobacter* strain isolated from agricultural crops showed high nitrogenfixing ability at 30% NaCl. The nitrogen fixation efficiency of a bacterium *A. vinellandii* was decreased from nonsaline to saline condition as reported by Sahoo et al. [\(2014\)](#page-28-5). *Azospirillum halopraeferens* was isolated and enhanced the growth of mangrove plant by root colonization irrigated with seawater (Bashan et al. [2000\)](#page-20-6). A little information is available on the halotolerant microbial diversity isolated from saline soils as compared with hypersaline aquatic locales (Oren [2008;](#page-27-2) Yang et al. [2016\)](#page-31-8).

#### **11.4 Effect of Soil Salinity in the Soil Environment**

The salinity soil is considered mainly as a major problem in the ecosystem because these problems increase continuously, disturbing biotic and abiotic soil constituents (Vandegehuchte et al. [2010;](#page-29-3) Bünemann et al. [2018\)](#page-21-12). It also affects natural circumstances in the barren and semi-barren regions of an ecosystem. Excess of saline soils affects seriously on the micro- and macro-floral structure and on space where it lives

(Getu [2009\)](#page-23-4). Excess salt in the soils known as sodic soils contains sodium and chloride ions in the earthen constituent part (Bianco and Defez [2010\)](#page-21-13). Due to insufficient discharge and drainage of irrigation water, salts accumulated in the soil (Cuevas et al. [2019\)](#page-22-5). However, the chlorides, bicarbonates of calcium, sulfates, carbonates, magnesium, sodium, and potassium salts are present in the irrigation water (Warrence et al. [2002\)](#page-30-9). The soil structure growth and the production of crops adversely are affected by salt concentration (Ondrasek et al. [2011;](#page-27-4) Shrivastava and Kumar [2015\)](#page-28-2). On the bases of soil and groundwater practices generally, the salinity is of three types: transient, groundwater associated, and irrigation salinities (Greene et al. [2016;](#page-23-5) Chandra et al. [2020\)](#page-21-14). Salinity affects both soil system and living organisms that are known as most severe abiotic environmental stress (Gupta and Huang [2014\)](#page-23-6). The immediate consequences of soil are found for biological activity or conservation occurs within the pore space or on the surfaces of the particles that forms the pores (Indoria et al. [2017;](#page-24-1) Totsche et al. [2018\)](#page-29-4). High salinity leads to negative effects on soil structure which is well known.

Soil dispersion and clay platelets to swell and aggregate are caused by elevated sodium concentrations (Warrence et al. [2002\)](#page-30-9). Thus, in the binding of clay particles, the forces involved are dislocated under the stimulus of sodium ions. Clay particles to plug soil pores are caused due to the dispersion of soil (Arora and Dagar [2019\)](#page-20-7). Therefore, the permeability of soil for water and air is reduced and forms apparent crusting (Kooistra and Tovey [1994;](#page-24-2) Greene and Hairsine [2004\)](#page-23-7).

It is documented that the presence of water in the soil leads to the swelling of the soil particles with high smectite clay content, and the hydration of some minerals as a result of the reduction of the cross-sectional area of soil pores is documented (Mahrous et al. [2018\)](#page-25-5). Under high sodium or low salt concentrations, this process is completed and it causes the mobilization of fine particles and diffusion within the pores (Mahrous et al. [2018;](#page-25-5) Chandra et al. [2020\)](#page-21-14). The water and air will be obstructed within the soil structure and particles by the particles stored in the small pores (Schjønning et al. [2002\)](#page-28-6).

# **11.5 Mechanisms for Adaptation of Microorganisms in the Hypersaline Environment**

Phylogenetically, the microbial life is very diverse at high concentrations, and the salinity environments are occupied by halophilic and halotolerant microflora of all domains of life, such as archaea, bacteria, and eukarya (Oren [2008;](#page-27-2) Ma et al. [2010\)](#page-25-6). Using this mechanisms these halophile microorganisms to tolerate the high salt concentrations, and in various cases to acclimatize their structure to alterations in high salinity in their environments, are miscellaneous as well (Oren [2008\)](#page-27-2).

The basic mechanisms for adaptation of microorganisms in the hypersaline environment are given below:

- Biological membranes of the microorganism are absorptive to water containing salt. Consequently, the movement of water inside and outside of microbial cells is possessed by changes in ionic activity between cytoplasm and external medium (Murínová and Dercová [2014;](#page-26-6) Watson [2015\)](#page-30-10).
- The bacterial cell maintains high osmotic pressure under saline condition; therefore, it is another strategy for adaptation mechanism (Weinisch et al. [2018\)](#page-30-11).
- The high concentrations of inorganic salts inside the microbial cell are accumulated and achieved the osmotic balance. The sodium ions are left out from cells in all three domains of life, and inside the cell the salt strategy is based on KCl rather than NaCl as a main salt of intracellular organism (Oren [2002\)](#page-27-5).
- Di-myoinositol-1, 1-phosphate, cyclic 2,3-diphosphoglycerate, α-diglycerol phosphate, mannosylglycerate, and mannosylglyceramide are compatible solutes which are very strong water structure formers and are excepted from the hydration shell of proteins, thus alleviating the hydration shell and decreasing the water activity coefficients (Gunde-Cimerman et al. [2018\)](#page-23-8).
- In many extremophiles, such low-molecular weight compounds are accumulated to increase the concentrations of salts but also as a reply to other ecological alterations such as temperature stress.
- Di-myoinositol-1, 1-phosphate, cyclic 2, 3-diphosphoglycerate,  $\alpha$ -diglycerol phosphate, mannosylglycerate, and mannosylglyceramide are the examples of organic compatible solutes in thermophiles and in psychrophiles (da Costa and Santos [2009\)](#page-22-6).
- Mostly, at low salt concentration, the microorganisms are endured and also accumulate salts inside the cell in the form of solutes from outside medium (Shrivastava and Kumar [2015\)](#page-28-2).

## *11.5.1 Mechanism of Salt Tolerance*

The microbial population in the rhizosphere decreases severely due to increase in pH and salinity (Ibekwe et al. [2010\)](#page-23-9). In hypersaline atmosphere the microbes inhabits using "compatible solute strategy" having capability to strong osmotic pressure to resist the salt stress (Pikuta et al. [2007;](#page-27-6) Chandra and Singh [2017\)](#page-21-15). Choline, betaine, proline, glutamic acid, and other amino acids are the compatible solutes stored by various halophilic bacteria at high concentrations without interfering with cellular processes (Poolman and Glaasker [1998\)](#page-27-7).

# *11.5.2 Characteristics and Function of Compatible Solutes*

The HPLC and NMR methods are followed for the determination and production of compatible solutes in various archaea and bacteria (Roberts [2005a,](#page-28-7) [b\)](#page-28-7). The compounds in limited numbers comprise the bacteria such as sugars (trehalose), polyols (glycerol and glucosyl glycerol), free amino acids (proline and glutamate), offshoots thereof (proline, betaine, and ectoine), quaternary amines and their sulfonium analogs (glycine betaine, carnitine, and dimethylsulfoniopropionate), sulfate esters (choline-O-sulfate), and N-acetylated diamino acids and small peptides (N-acetylornithine and N-acetylglutaminylglutamine amide) (Kempf and Bremer [1998\)](#page-24-3). Generally, the compatible solutes do not carry a net charge at physiological pH due to their high molecular solubility (Galinski [1993\)](#page-22-7). The vital cellular functions such as DNA replication, DNA–protein interactions, and the cellular metabolic machinery without disturbing the solutes can reach high intracellular concentrations in disparity to mineral salts (Wang and Levin [2009;](#page-30-12) Long et al. [2018\)](#page-25-7). Compatible solutes such as glycine, betaine, and proline increase the cytoplasmic volume and water content freely of the cells at high osmolality, and their accumulation uninterruptedly permitted proliferation of cells under unfavorable conditions (Kohler et al. [2015\)](#page-24-4).

Various halotolerant nitrogen-fixing bacteria accumulate electrolytes such as  $K^+$ glutamate, as enzymes, ribosomes, and transport proteins of these bacteria require high level of potassium for stability and activity using salt in strategy mechanism (Da Costa et al. [1998a,](#page-22-8) [b\)](#page-22-9). But within the cell physiology, organic solute accumulations are more compatible (Ventosa et al. [1998;](#page-30-7) Wood et al. [2001\)](#page-30-13). The organic solutes have two mechanisms under saline conditions for their mode of actions: firstly to increase the intracellular osmotic strength and secondly to stabilization; the cellular macromolecules are proposed (Yancey et al. [1982;](#page-31-9) Csonka [1989;](#page-22-10) Chandra and Enespa [2019a\)](#page-21-16). After adding these solutes in bacterial culture, the drastic stimulation in growth rate is observed in cells in high osmolality media (Gouffi et al. [1998\)](#page-23-10). Higher internal concentrations of solutes accumulated in the alleviation of osmolality (Patchett et al. [1992\)](#page-27-8). The glucose is oxidized in Entner–Doudoroff pathway modifications by the mostly halotolerant organisms (Fig.  $11.1$ ), the synthesis of compatible solutes after formation of pyruvate, and its further oxidation by pyruvate oxidoreductase in tricarboxylic acid cycle (TCA) (Kindzierski et al. [2017\)](#page-24-5).

In salt-tolerant bacteria, the accumulation of organic solutes has been found to require genetic initiation (Roberts [2005a,](#page-28-7) [b\)](#page-28-7). In response to osmotic stress in *Bacillus* sp., intracellular proline to increase rapidly has been observed and the corresponding genes were detected, respectively, proB, proA, and proC encoding γglutamyl kinase ( $γ$ -GK),  $γ$ -glutamyl-phosphate reductase ( $γ$ -GPR), and pyrroline-5-carboxylate (P5C) reductase (Pérez-Arellano et al. [2010\)](#page-27-9). L-aspartokinase (Ask), L-2,4-diaminobutyric acid transaminase (EctB), L-2,4-diaminobutyric acid acetyltransferase (EctA), and L-ectoine synthase (EctC) encoding the structural gene and detected for biosynthesis of major harmonious solute like ectoine in *Halobacillus dabanensis*(Reshetnikov et al. [2006;](#page-28-8) Czech et al. [2019\)](#page-22-11). Choline or choline-O-sulfate oxidized enzymatically into glycine betaine due to involvement of four genes *betI,*



<span id="page-7-0"></span>**Fig. 11.1** Synthesis of compatible solutes: Proline, ectoine, and glutamine under stress conditions (Figure adopted by Saum and Müller [2008\)](#page-28-9)

*betC, betB,* and *betA* well characterized at molecular level and organized into one operon (Osteras et al. [1998;](#page-27-10) Stöveken et al. [2011\)](#page-29-5). Various halotolerant nitrogenfixing bacteria are also observed in the cell for the maintaining of the balance of Na<sup>+</sup> and K<sup>+</sup> ions (Hanin et al. [2016;](#page-23-11) Thomas and Apte [1984\)](#page-29-6). A cytoplasmic KCL concentration is maintained by bacteria similar to that of the surrounding medium in order to attain an osmotic equilibrium (Kraegeloh et al. [2005\)](#page-25-8). The  $Na<sup>+</sup>/H<sup>+</sup>$  antiporter performance is a major character in homeostasis of  $pH$  and  $Na<sup>+</sup>$  in cells that interchange Na<sup>+</sup> for H<sup>+</sup> (Suárez et al.  $2008$ ). The genes that are proved to be involved in halotolerance in nitrogen-fixing bacteria either through knockout studies or through overexpression studies are framed in Table [11.1.](#page-8-0)

# *11.5.3 Exchange of Solutes/Ions*

Many solutes/ions are present in the soils and perform an important character in the existence of microorganisms in the presence of soil salinity (Shrivastava and Kumar [2015\)](#page-28-2). However, more solutes or ions containing soils can decrease microbial population in the rhizospheric region of plants (Aung et al. [2018\)](#page-20-8). Several microbes reside in hypersaline environment condition proficient passionate osmotic pressure, and thus use compatible solute strategy or salt-in strategy to resist salt stress (Oren [2011\)](#page-27-11). Choline, betaine, proline, glutamic acid, and other amino acids compatible solutes accumulated in most of the bacteria at high salinity without interfering with cellular procedures (Wood et al. [2001\)](#page-30-13).

<b>Strains</b>	Products	Genes	References
Rahnella aquatilis HX2	1-aminocyclopropane-1- carboxylic acid deaminase	acdS gene	Peng et al. (2019)
Sinorhizobium meliloti <b>B401</b>	$Na^+/H^+$ antiporter	AtNHX1 gene	Stritzler et al. (2018)
Azospirillum lipoferum FK1	Proline and glycine betaine levels	PAL, PPO, CHS, CHI, REB2A, and <b>IFS</b>	El-Esawi et al. (2019)
Klebsiella sp. SBP-8	$K^+ / Na^+$ transporters	AcdS gene	Singh et al. (2015)
Pseudomonas aeruginosa	$Na^+/H^+$ antiporter	nhaP	Inaba et al. $(2001)$
Sinorhizobium meliloti	(p) pp Gpp synthetase	relA	Wei et al. (2004)
	Glycine betaine/proline	bet genes	Mandon et al. (2003)
	Betaine transporter	betS gene	
	Transcription cleavage factor	greA	
	Potassium-uptake protein	Kup	Nogales et al. (2002)
Rhizobium tropici	Histidine kinase $Na^+/H^+$ antiporter	ntrY, ndvA and ndvB (synthetic gene), nhaA, nhaB, nhaC	Wai Liew et al. (2007)
Azotobacter vinelandii	Glucosyl glycerol biosynthesis	ggpPS	Klähn et al. (2009)
Enterobacter cloacae	$Na^+/H^+$ antiporter	nhaA	Lentes et al. $(2014)$
Synechocystis sp.	$Na^+/H^+$ antiporter	nhaS1, nhaS2, nhaS3, nhaS4, and nha <sub>S5</sub>	Mitschke et al. (2011)
Aphanothece halophytica	$Na^+/H^+$ antiporter	napA	Laloknam et al. (2006)
<b>Bacillus</b> subtilis	$\gamma$ -glutamyl kinase	proA, proBproC	Zhao et al. $(2011)$

<span id="page-8-0"></span>Table 11.1 Genes conferring salt tolerance response in selected nitrogen-fixing bacteria

# *11.5.4 Mechanism of Salt-Dependent Lipid Changes*

The lipid content present in the microbial plasma membrane shows special character for the survival of stress environmental condition. The phospholipids of *Pseudomonas halosaccharolytica* contain glucosyl phosphatidylglycerol, phosphatidylglycerol, diphosphatidylglycerol, and phosphatidylethanolamine which are responsible for growth under high saline condition (Li et al.  $2016$ ), and this result indicates increase of phosphatidylglycerol and reduction in phosphatidylethanolamine (Hiramatsu et al. [1980\)](#page-23-13). Later, Hara and Masui [\(1985\)](#page-23-14) observed that pulse-chase labeling of lipids with several radioactive originators showed that the rate of synthesis of phosphatidylethanolamine was inhibited by an increase in salt concentration, but the rate of phosphatidylglycerol synthesis was unaffected. The deficiency of motivation of phosphatidylglycerol creation by salt does not settle with compositional data. The radiolabeling experimentations were performed with nongrowing, starved cells, whereas the compositions of lipids were resolute directly on cells collected from culture media (Hara and Masui [1985\)](#page-23-14). The inhibition of phosphatidylethanolamine creation leads to an upsurge in phosphatidylglycerol comfortable in the microbial cell because of the bifurcated phospholipid biosynthetic pathway going inside the cell (Sohlenkamp and Geiger [2016\)](#page-28-11). A similar type of study was performed by Ohno et al. [\(1979\)](#page-26-10); the little amount of NaCl did not affect the growing bacteria due to the presence of glucosyl phosphatidylglycerol. However, survival mechanisms of halophilic bacteria due to membrane lipid composition cannot judge very easily; this is a very difficult process (Oren [2008\)](#page-27-2). The lots of chemicals, labor, and time may be taken to well understand the interaction between bacterial lipid membrane and salt medium (Pichler and Emmerstorfer-Augustin [2018\)](#page-27-13).

## *11.5.5 Salt-Tolerant Genes of Bacteria*

Many microorganisms contain salt-tolerant gene and perform an important character in survival for extreme environmental condition especially salt (Holmberg and Bülow [1998\)](#page-23-15). The bacterial spores of *Bacillus thuringiensis israelensis, B. sphaericus,* and *B. subtilis* contain osmotolerant protein, i.e., small acid-soluble spore protein (SASP) coded by an ssp gene and this gene can survive at the high salt concentration (Cucchi and Rivas [1995\)](#page-22-12). Cucchi and Rivas [\(1995\)](#page-22-12) reported a sspE gene from *B. subtilis* and is introduced into another host bacterium *B. thuringiensis israelensis* strain 4Q2 and observed 65–650 times higher level of salt-tolerant property as compared to natural *B. thuringiensis israelensis.* In addition, this bacterium does not cause any side effects in living organisms as well as environments. Some other genes such as ectA (diaminobutyric acid acetyltransferase), ectB (diaminobutyric acid aminotransferase), and ectC (ectoine synthase) genes are reported in *B. halodurans* and showed in the survival of stress tolerance (Reshetnikov et al. [2011\)](#page-27-14).

There are two genes, namely, GspM and EchM have recognized from a metagenomic collection organized from water sample of pond (Kapardar et al. [2010\)](#page-24-7). GspM gene displays comparison with stress proteins, and another gene EchM showed similarity with enoyl-CoA hydratases and both genes were identified to be responsible for halotolerant at high concentration and have latent solicitation in generating halotolerant recombinant bacteria or transgenic crops (Kapardar et al. [2010\)](#page-24-7). The two genes were further isolated from *Rhizobium* sp. BL3 and showed hyper-salt-tolerant ability (Payakapong et al. [2006\)](#page-27-15). Hence, many microbes from rhizosphere can be exploited to isolate novel gene for salt tolerance and their potential application in the plant genetic engineering or plant growth under saline environment condition.

# *11.5.6 Salt-Tolerant Genes of Yeast*

The two genes HAL1 and HAL3 were isolated and showed overexpressed gene from yeast (*Saccharomyces cerevisiae)* and also increased the halotolerant capability by a decreasing intracellular  $Na<sup>+</sup>$  and enhanced internal  $K<sup>+</sup>$  concentration during salt stress (Ferrando et al. [1995;](#page-22-13) Locascio et al. [2019\)](#page-25-12). Further, the gene HAL1 has been introduced into tomato crop by *Agrobacterium tumefaciens*-mediated transformation which improves salt tolerance of the transgenic tomato and enhances the growth and productivity (Gisbert et al. [2000\)](#page-23-16). An enzyme mitogen-activated protein kinase (MAPK) coded by a gene HOG1 shows an important role in the osmoregulatory pathway in *S. cerevisiae* (O'Rourke and Herskowitz [1998\)](#page-26-11). This gene is also responsible for salt tolerance in *Torulopsis versatilis* (Wang et al. [2014\)](#page-30-16). A delightful mutant strain *Torulopsis versatilis* T5 showing salt-tolerant ability was fashioned from wild-type *T. versatilis* (T) consuming genome trundling and further isolated two genes T5HOG1 and THOG1, demonstrating upturn of salt tolerance in *T. versatilis* (Cao et al. [2011\)](#page-21-17). Moreover, overexpression of T5HOG1 and THOG1 enhanced the acceptance of salt in *S. cerevisiae* (Cao et al. [2011\)](#page-21-17).

# *11.5.7 Salt-Tolerant Genes of Plants*

A wide range of cruel ecological circumstances such as salinity, heat, cold, drought, and insect attack are normally exposed in plants. Plants have established altered methods being in sessile nature to survive grow and develop under speedily altering environmental conditions (Hayat et al. [2012\)](#page-23-17). For these mechanisms, plants regulate genes for transcription which are known as transcriptomics under stress conditions (Shu et al. [2018\)](#page-28-12). The genes for regulation of transcription play different roles under stressful environmental conditions. However, during the reproductive and seedling stages, plants have more sessile to stress and the stress response studies express novel genes or proteins with imperative roles in plant anxiety reworking during these growth stages (Verma et al. [2016a,](#page-29-9) [b\)](#page-29-10). However, the word salinity acceptance comes from one or more genes that reduce the uptake of the salt content from the soil and the conveyance of salt through the plant (Munns [2005,](#page-26-12) [1993\)](#page-26-13).

Salinity tolerance is a very complex process that is recycled by plants to regulate (up-regulation or down-regulation) the manufacture of specific gene products in the form of RNA or proteins (Gupta and Huang [2014\)](#page-23-6). This process has been accepted at different stages of central dogma technologies like from initiation of RNA processing, post-transcriptional modification, and initiation translation to post-translational modification of proteins in living organisms especially plants (Zhao et al. [2017\)](#page-32-1). Understanding the transcription or translation of plants delivers thorough knowledge about the gene expression at the mRNA level. The summary of transcriptional or translational level is widely used for isolation and identification of candidate genes involved in stress responses (Xiao et al. [2017\)](#page-30-17).

Transcriptome profiling is the screening processes which down-regulated or upregulated the transcription processes that are enormous evidence about salt-tolerant genes till now. Further, a genomic method gives an important role in cloning, encoding, screening, and identifying these genes (Lodish et al. [2000\)](#page-25-13). Under salt stress condition, the expression of gene is altered by transcript issues and those up- or down-regulated the expression of the gene in plants or microorganisms by these are most important switches (Lodish et al. [2000\)](#page-25-13).

A gene bZIP was identified and showed up-regulation gene expression in wheat crop under insistent salt stress disorder and gene expression of down-regulation in salt-tolerant variety of wheat crop (Hayano-Kanashiro et al. [2009\)](#page-23-18). The osmotic regulating and ROS-scavenging genes mostly are salt tolerance genes and also upregulated in salinity toleant species (Amirbakhtiar et al. [2019\)](#page-20-9). According to study, more than 10 genes showed up-regulated genes in halophytes plant species *Spartina alterniflora* under saline condition. Under saline condition, more than 10 genes showed up-regulated genes in *Spartina alterniflora* halophytes plant species, and most of the genes were found to osmotic regulation process among them (Bedre et al. [2016\)](#page-20-4).

# **11.6 Mechanisms of Plant Growth Promotion of Halophilic Bacteria**

## *11.6.1 Nitrogen Fixation Under Salt Stress Condition*

At global level in arid and semi-arid regions, salinity is a serious issue for agriculture. Growth promotion and photosynthesis rate at various stages of plants affected by salinity stress (Magallon and Dinneny [2019\)](#page-25-0). The production of salt-sensitive crops such as legumes is affected by salt stress particularly since these plants depend on nitrogen requirement for symbiotic  $N_2$  fixation (Hussain et al. [2010;](#page-23-19) Kour et al. [2019b,](#page-24-8) [c,](#page-24-9) [d\)](#page-25-14). The crop productivity mainly depends on the deprived mutual association of nodulation in bacteria and ultimately decreases in nitrogen fixation capacity (Mengel et al. [2001\)](#page-26-14). *Vicia faba, Phaseolus vulgaris,* and *Glycine max* legume plants are more salt-tolerant species than another leguminous plant *Pisum sativum* (Mengel et al. [2001\)](#page-26-14). *V. faba* crop fixed more nitrogen under saline condition due to the presence of rhizobia inside the root nodules and it has been seen (Mengel et al. [2001\)](#page-26-14). *Prosopis*, *Acacia*, and *Medicago sativa* are the other salt-tolerant leguminous plants but these are less halotolerant than the leguminous plants (Joseph et al. [2015\)](#page-24-10). *Rhizobium* sp. performs a very significant character in symbiosis with plants and nodulation process but, in the presence of salt, inhibits the initial process of rhizobium–legume symbiosis (Maróti and Kondorosi [2014\)](#page-26-15). However, in several reports, the effect of salt stress on nodulation and nitrogen fixation of legumes have been observed (Maróti and Kondorosi [2014\)](#page-26-15). In the presence of salt, the capability of  $N<sub>2</sub>$ -fixation reduces and is documented to a decrease in the respiration of the nodules and minimize in cytosolic

production protein, especially leghaemoglobin by nodulation (Zahran [1999\)](#page-31-10). Saline stress negatively affected on  $N_2$  fixation by legumes is related to the salt-induced decline directly in dry weight and nitrogen content in plant shoot (Delgado et al. [1994\)](#page-22-14).

Glycine betaine is the osmoprotective substances which perform an imperative character in the maintenance of nitrogenase activity in bacteroides under salinity stress (Normand et al. [2015\)](#page-26-16). The halotolerant *Rhizobium* sp. enhanced the growth, nodulation, and fixed  $N_2$  content in *Acacia ampliceps* plant containing 200 mM NaCl concentration in the sand culture medium (Egamberdieva et al. [2013\)](#page-22-15) and one more halotolerant *Rhizobium* sp. designed  $N_2$  fixing symbiosis more effective with soybean than other salt-sensitive strain of bacteria (Egamberdieva et al. [2013\)](#page-22-15). Further, the isolated rhizobial strains from *Acacia nilotica* showed tolerance to 850 mM NaCl concentration formed effective N<sub>2</sub>-fixing nodules on *Acacia* trees grown at 150 mM NaCl (Zahran [1999\)](#page-31-10). The salt-tolerant *Rhizobium* strains produce nodulation in legumes and form effective  $N_2$  fixing symbiosis capability in the soil under moderate halophile environment observed in the result (Zahran [1999\)](#page-31-10). Therefore, the booster of salt-tolerant rhizobia strains in the rhizosphere of leguminous crop can enhance the  $N_2$  fixation ability under saline condition. However, host tolerance legume to NaCl is a very key element in influencing the achievement of harmonious *Rhizobium* strains to form symbiosis successfully under the halophilic environment (Egamberdieva et al. [2013\)](#page-22-15).

#### *11.6.2 Phytohormone Production Under Saline Condition*

Phytohormones are natural organic compounds which enhance the growth and productivity of cultivars at very less concentrations. These phytohormones support the distinction and improvement of plant growth by the regulation of various progressions. Generally, the phytohormones at plants root locality are the microbial origin recommended for a functional reply in the host crop (Verma et al. [2016a,](#page-29-9) [b;](#page-29-10) Enespa and Chandra [2019\)](#page-22-16). Indole-3 acetic acid (IAA), gibberellic acid, abscisic acid (ABA), cytokinins, and other plant growth regulators produced by NaCl-tolerant rhizobacteria outwardly maintain the rooting with augmented number of roots, increase root length, shoot length, and number of root tips, and finally lead to increase in the uptake of nutrients and thus progress plant fitness under saline environmental circumstances (Verma et al. [2016a,](#page-29-9) [b\)](#page-29-10). *Bacillus* and *Pseudomonas* strains belong to IAA production that improved the growth of soybean crop at 100 mM NaCl concentration by the increasing antioxidant activity and decreasing the lipid peroxidation (Kumari et al. [2015\)](#page-25-15). Furthermore, an isolated bacterium produced osmotolerant IAA displayed to increase the sprouting of rice seeds in salinity stress are reported (Jha and Subramanian [2013\)](#page-24-11).

# *11.6.3 ACC Deaminase Production Under Saline Condition*

A volatile phytohormone known as ethylene has capacity for growth promotion of plant at very less quantity like nodulations and improvement of various asexual plant parts, rooting, cuttings, and also twisted in the transduction of a signal for the appreciation of saline stress ecosystem (Saravanakumar and Samiyappan [2007\)](#page-28-13). However, a large amount of ethylene is produced under abiotic environmental ecosystem and in the presence of this substrate can inhibit the root growth, shoot growth, and productivity of plants (Morgan and Drew [1997\)](#page-26-17). Some chemical substrates such as aminoethoxyvinylglycine and cobalt ions act as an inhibitor of ethylene synthesis (Arora et al. [2017\)](#page-20-10).

However, these chemical substrates are too much expensive and also can harm plants and environment. Halotolerant rhizobacteria showing plant growth-promoting characters contain aminocyclopropane-1-carboxylate (ACC) deaminase which splits ACC into ammonia and α-ketobutyrate, thereby reducing the near of ethylene in stressed plants (Habib et al. [2016\)](#page-23-2). In the presence of ACC deaminase-producing bacteria, plant 1-aminocyclopropane-1-carboxylate is sequestrated and ruined by the cells of bacteria to fund energy and nitrogen, enhancing the plant growth under saline ecosystem (Tiwari et al. [2018\)](#page-29-11).

The rhizospheric bacteria which belong to Gram-positive and Gram-negative genera such as *Arthrobacter, Bacillus, Brevibacterium, Corynebacterium, Exiguobacterium, Halomonas, Micrococcus, Oceanimonas, Planococcus,* and *Zhihengliuella* have been widely reported for ACC deaminase activity under saline conditions and have recognized as a potential role in enhancement of growth under saline ecosystem through ACC deaminase activity (Siddikee et al. [2015;](#page-28-14) Yadav et al. [2019c,](#page-31-11) [d,](#page-31-12) [e\)](#page-31-13). *Pseudomonas simiae* strain AU5 is the mutant bacterium overproduced ACC deaminase documented to alleviate salt stress in mung bean plants as compared to wild strain *P. simiae* AU5 and observed decrease the concentration of ethylene and salt-induced membrane (bacteria and plants) damage (Kumari et al. [2016\)](#page-25-16).

#### *11.6.4 Under Salt Condition Phosphate Solubilization*

Phosphorus (P) is an indispensable mineral after nitrogen for the growth of plant promotion as it and essential of dissimilar biomolecules such as nucleic acids, nucleotides, phospholipids, and phosphoproteins (Sharma et al. [2013\)](#page-28-15). In the presence of salinity, uptake of P in plants is reduced and deficiency of P is appeared in the form of symptoms such as dark bluish-green in color with leaves and stem becoming purplish, etc. (Sharma et al. [2013\)](#page-28-15). Mostly, insoluble forms of phosphorus in soils, i.e., organic and inorganic phosphate, have less mobilization in the soils (Sharma et al. [2013\)](#page-28-15). Insoluble organic and inorganic phosphate conversion can be possible due to species of rhizobacteria and also helps in the translocation of P from soil to roots. For the solubilization of insoluble phosphates, many rhizobacteria show one of the several mechanisms such as reactions of ion-exchange, chelation, acidification, and the production organic acids of low molecular weight such as gluconic acids (Kalayu [2019;](#page-24-12) Rana et al. [2019a,](#page-27-16) [b;](#page-27-17) Verma et al. [2017a\)](#page-29-12). The halotolerant rhizobacteria to be vital for the mobilization of plant nutrients in several types and reduced the acceptability of inorganic fertilizers (Jiang et al. [2019\)](#page-24-13).

However, phosphate solubilization is a common process in the rhizosphere by rhizobacteria that upsurge the mineral accessibility to crop (Jiang et al. [2019\)](#page-24-13). An important role played by the rhizospheric bacteria to the regulation of P from less available forms and are essential for sustaining P is voluntarily available pools. Upadhyay et al. [\(2011\)](#page-29-13) reported rhizobacterial strains to have well-organized solubilizing ability of phosphate even up to high saline (6% NaCl concentration) condition and enhanced plant growth under similar condition. For example, *Pseudomonas* inoculated in the rhizosphere of *Zea mays* crop showed salt tolerance under 6% NaCl stress condition and increased the crop growth at same salt condition (Bano and Fatima [2009\)](#page-20-11). Additionally, *Herbaspirillum seropedicae* and *Burkholderia* sp. are the phosphate dissolving bacteria; treated plants recorded 1.5–21% dry weight as a compared to control plant under saline condition. Afterward, the better germination of root and shoot growth as compared with control plant after being exposed to NaCl inoculated *Azospirillum* in lettuce seeds (Carrozzi et al. [2012\)](#page-21-18). *P. simiae* solubilizes phosphate by producing acid phosphatase activity along with volatile compounds that enhanced plant storage protein and uptake of P in soybean plants under 100 mM NaCl saline ecosystem (Vaishnav et al. [2015\)](#page-29-14).

#### *11.6.5 Antioxidative Response Under Salt Condition*

The compounds inhibit oxidation reaction known as an antioxidant, and this is a chemical/biochemical process that can produce free radicals (Lü et al. [2010\)](#page-25-17). The oxidative stress is caused by the abiotic environmental factor like drought and saline soil and resulted in the formation of reactive oxygen species (ROS) such as singlet oxygen (O2), hydrogen peroxide (H2O2), and hydroxyl radical (−OH) that damage cellular membranes, proteins, and DNA (Nita and Grzybowski [2016\)](#page-26-18). When the level of ROS increases, this causes oxidative damage to biomolecules such as lipoproteins and at last leads to the death of plants (Sharma et al. [2012\)](#page-28-16). However, some major antioxidative enzymes such as superoxide dismutase (SOD), peroxidase (POX), and catalase (CAT) are produced by rhizospheric bacteria such as *Streptococcus. Proteamaculans*, and *Rhizobium leguminosarum,* and non-antioxidant enzymes/compounds like ascorbic acid, tocopherols, and glutathione contribute in ROS-scavenging mechanism (Sharma et al. [2012\)](#page-28-16). Mycorrhizal-inoculated lettuce plants showed higher superoxide dismutase (SOD) activity and protect the plant in the presence of antioxidant under drought stress condition (Ruiz-Lozano [2003\)](#page-28-17).

Salt resistance plants have been associated to more effective antioxidant schemes, and a salt-tolerant bacterium *P. simiae* strain AU enriched antioxidants (peroxidase and catalase) and gene expression in soybean plants when treated with 100 mM NaCl

stress disorder (Vaishnav et al. [2016;](#page-29-15) Chandra and Enespa [2019c\)](#page-21-19). Drought stress effects in maize plants are alleviated by *Pseudomonas* spp. drought-tolerant rhizobacteria due to decrease in the antioxidant enzyme activity (Afridi et al. [2019\)](#page-20-12). The catalase and peroxidase activity boosted the non-inoculated crops during saline soil, whereas *Azospirillum brasilense* inoculated plants showed lower enzyme activity and expressively ameliorated the deleterious effects of salinity (Omar et al. [2009\)](#page-27-18).

#### *11.6.6 Siderophore Production Under Salt Condition*

In the chelation of micronutrients, siderophore plays an imperative character such as iron even under limiting conditions and with the redox activity it serves as a cofactor of many enzymes (Ahmed and Holmström [2014;](#page-20-13) Chandra and Enespa [2016\)](#page-21-1). Several studies are reported on *Bacillus* to be a good siderophore producer (Kesaulya et al. [2018\)](#page-24-14). Production of siderophores in the rhizosphere by bacteria also helps in dissolving of other ingredients, for example, P, zinc, potassium, and the availability of various ionic ingredients to the plant through chelation of iron from precipitated form (Sharma et al. [2013;](#page-28-15) Ahmed and Holmström [2014\)](#page-20-13). In the soils, a huge amount of iron is existent, but in an extremely unsolvable ferric hydroxide form, hence the performances of iron as a limiting factor for promotion of plants growth even in ironic soil. However, ferrous ( $Fe^{++}$ ) iron is oxidized into ferric ( $Fe^{+++}$ ) form by oxidation process (Kesaulya et al. [2018\)](#page-24-14). Under the biological ecosystem, the ferric ions are inexplicable which forms its achievement by microorganisms, a considerable challenge in the soils (Colombo et al. [2014\)](#page-22-17). Siderophores play important roles in the development of plant growth by rhizospheric microorganisms (Ahmed and Holmström [2014\)](#page-20-13). Plants and bacteria mediate competition using existence of siderophore that results in exclusions of fungal pathogens and other microbial competitors in the rhizosphere by a reduction in the availability of iron for their survival (Ahmed and Holmström [2014\)](#page-20-13).

## *11.6.7 Halophilic Microbes as Biocontrol Agents*

The production of crop yield potentially increased, and its diseases controlled biologically from rhizospheric microflora. Inhibition of phytopathogens using rhizobacteria compromises a more sustainable method to control infection as compared to harmful chemical-based methods (Compant et al. [2010;](#page-22-18) Etesami and Alikhani [2018\)](#page-22-19). Under the saline condition, a halophilic microbe plays an important role in maintaining morphology, physiology, and reduction in soil salinity and also increases plant susceptibility against phytopathogens (Table [11.2\)](#page-16-0) (Etesami and Beattie [2018\)](#page-22-3).

Halophilic microbes use to hostage the injurious properties of plant pathogens through different mechanisms. Halophilic microbes produce one or more antimicrobial metabolites that act as antifungal, antibacterial, antiviral, antioxidant, cytotoxic,

Microbes	<b>Host Plants</b>	Effect of host plants under saline condition	Salt concentration	References
Bacillus pumilus ST2	Oryza sativa	Controlling caspase-like activity, programmed cell death, antioxidative activity	25 mM NaCl	Jha et al. (2011)
B. pumilus STR2. Exiguobacterium oxidotolerens STR <sub>36</sub>	Bacopa monnieri L.	High proline content/lipid peroxidation	4 g NaCl/Kg of soil	Bharti et al. (2013)
Burkholderia phytofirmans PsJN, Enterobacter sp. FD 17	Zea Mays	Decreasing xylem Na <sup>+</sup> concentration/maintain nutrient balance within the plants	25 mM NaCl	Akhtar et al. (2015)
<b>B.</b> pumilus STR2, Halomonas desiderata STR8	Zea mays	Preventing major shifts indigenous microbial community	50 mM NaCl	Bharti et al. (2015)
P. simiae strain AU-M4	Glycine Max L.	Inoculated reduced $Na+$ and enhanced $K+$ uptake	100 mM NaCl	Vaishnav et al. (2015)
Acinetobacter sp. ACMS25, Bacillus sp. PVMX4	Phyllanthus amarus	Improved antioxidative defense system	160 mM NaCl	Joe et al. (2016)
P. fluorescens 002	Zea Mays	Improved root growth and root formation under salt stress	150 mM NaCl	Zerrouk et al. (2016)
Azotobacter chroococcum AZ6	Zea mays	Improved chlorophyll a and total content, reduced proline and amino-acid content	20 mM NaCl	Silini et al. (2016)
Bacillus aquimaris DY-3	Zea mays L	Chlorophyll content, leaf relative water content, accumulation of proline, soluble sugar and total phenolic compound, and activities of superoxide dismutase, catalase, peroxidase, and ascorbate peroxidase were enhanced	1% NaCl	Li and Jiang (2017)

<span id="page-16-0"></span>**Table 11.2** Plant growth promotion of plants by halotolerant rhizobacterial inoculation

(continued)

<b>Microbes</b>	<b>Host Plants</b>	Effect of host plants under saline condition	Salt concentration	References
Bacillus sp., Actinomycetes sp., Rhizobium sp., Oceanospirillum sp.	Paddy crop	Improve rice germination, energy or germination capacity	$3-12$ g/L NaCl	Shi-Ying et al. (2018)
<b>Bacillus</b> subtilis (BERA 71)	Chickpea crop	Enhanced plant biomass and the synthesis of photosynthetic pigments and reduced the levels of reactive oxygen species (ROS) and lipid peroxidation in plants under conditions of stress.	200 mM NaCl	Abd Allah et al. (2018)
Pseudomonas <b>PS01</b>	Arabidopsis thaliana	Improve the germination rate, transcriptional levels of genes	150 mM NaCl	Chu et al. (2019)
Enterobacter aerogenes LJL-5 and Pseudomonas aeruginosa $LJL-13$	alfalfa plants	Increased the shoot height, fresh and dry weights, yield and crude protein content	150 mM NaCl	Liu et al. (2019)

**Table 11.2** (continued)

phytotoxic, and/or antitumor mediators (Olanrewaju et al. [2017\)](#page-26-19). *Bacillus* and *Pseudomonas* bacterial genera secreted this type of metabolites. Halophilic microbes are also able to produce enzymes such as lipase, cellulase, β-1, 3-glucanase, chitinase, and protease which can degrade cell wall and fungal growth (Husson et al. [2017;](#page-23-20) Vaddepalli et al. [2017\)](#page-29-16). Halophilic microbes compete for nutritive ingredients or for sites binding on roots of plants, and this type of antagonism reduces the growth of phytopathogen or mandatory destroyed proliferation of plant–pathogen (Olanrewaju et al. [2017\)](#page-26-19). Halophilic microbes such as *Alcaligenes*, *Aeromonas, Bacillus, Rhizobium,* and *Pseudomonas* can produce hydrogen cyanide production, and the presence of this chemical substance may control phytopathogens (El-Rahman et al. [2019;](#page-22-20) Suman et al. [2016;](#page-29-17) Verma et al. [2018;](#page-30-18) Yadav et al. [2018c\)](#page-31-14).

Halophilic microbes activate induced systemic resistance and enhance immunity against phytopathogens (Olanrewaju et al. [2017\)](#page-26-19). Halophilic microbes disrupt signaling pathways of phytopathogens by quorum quenching approach. For interference of signal pathways to minimize pathogen virulence, some specific degrading enzymes, such as lactonase, are responsible (Olanrewaju et al. [2017\)](#page-26-19). Halophilic microbes synthesized siderophore and inhibited the proliferation phytopathogens

due to decrease in the iron availability to phytopathogens (Ahmed and Holmström [2014\)](#page-20-13). The halophilic microbes provide biocontrol of phytopathogens by the production of antibiotics and antifungal metabolic substances. *Fusarium sambucinum*, *F. roseum* var.*sambucinum, F. oxysporum, F. moniliforme, F. graminearum, Penicillium citrinum*, *Aspergillus flavus*, and *Botrytis cinerea* are phytopathogenic fungi that are controlled by halophilic rhizospheric bacteria *B. subtilis, B. cereus*, *B. pumilus*, *B*. *licheniformis, C. alkalitolerans, Halomonas elongate*, and *Halobacillus halophilus*, *Halobacillus faecis*, *Salinicoccus roseus* (Ahmed and Holmström [2014;](#page-20-13) Olanrewaju et al. [2017;](#page-26-19) El-Rahman et al. [2019\)](#page-22-20).

# **11.7 Role of Halophilic Microbes in Sustainable Agriculture**

Chemical fertilizers and pesticides are commonly used by the farmers for improvement of soil fertility, growth, and productivity of crops under salt-based and nonsalt-based ecosystem (Ju et al. [2018\)](#page-24-17). But their regular use causes an adverse effect on living organism and soils (Bernardes et al. [2015\)](#page-20-18). Apart from these, chemical fertilizers remediate in the crop which feed by the organisms and ultimately reach to top consumers and cause numerous diseases (Gonçalves et al. [2014\)](#page-23-21). However, many transgenic salt-tolerant crops have been developed but far too little is successful (Bharti et al. [2016\)](#page-20-19). An alternative method is available which could replace chemical fertilizers and pesticides and also improve soil health, seed germination, crop growth, and productivity by rhizospheric bacteria (Vejan et al. [2016\)](#page-30-19). These rhizospheric bacteria enhance the growth and improvement of plants either straight or circuitously by colonizing the plant root (Vejan et al. [2016;](#page-30-19) Kour et al. [2019b;](#page-24-8) Yadav et al. [2019b\)](#page-31-15).

The uninterrupted character of PGPRs involves the fixation of nitrogen  $(N_2)$  secretion of metabolites, for instance, the indole-acetic acid (IAA) production, ammonia, solubilization of phosphate, siderophore, and zinc (Ahemad and Kibret [2014;](#page-20-20) Chandra and Enespa [2016\)](#page-21-1). Indirect growth promotion can be observed in the prevention and reduction of phytopathogens in plants through biocontrol mechanism. In this mechanism, PGPRs produce some lytic enzymes for fungal pathogens (cellulase, β-1, 3 glucanase, chitinase, and 1-aminocyclopropane-1-carboxylate (ACC) deaminase), reduction of iron (Fe) from the soil/rhizosphere and hydrogen cyanide (HCN), salicylic acid, antibiotics, or antifungal compounds (Odoh [2017;](#page-26-20) Chandra and Enespa [2019a,](#page-21-16) [b,](#page-21-9) [c\)](#page-21-19). Besides, PGPRs also accepted as capable rhizobacteria that can tolerant environmental stresses such as high salt, high temperature, and pH (Ahemad and Kibret [2014\)](#page-20-20).

The plant growth-promoting rhizobacteria enhance nutrient availability that includes nitrogen fixation and phosphate-solubilizing microorganisms. In indirect means, it reduces the deleterious effect of plant pathogens on crop yield (Ahemad and Kibret [2014\)](#page-20-20). It shows antagonism against phytopathogenic microorganisms by

producing siderophore (Vejan et al. [2016\)](#page-30-19). PGPR have been developed and used as biofertilizers. Biofertilizers containing these PGPRs are economical, environmentfriendly, and potentially renewable source of necessary enriched plant nutrients that makes it an excellent substitute of harmful fertilizers and chemical (Vejan et al. [2016\)](#page-30-19).

The mechanism-based action can be differentiated into three dissimilar groups, i.e, (1) Biofertilizer, containing PGPR having  $N_2$  fixation and P solubilization capability, (2) biopesticide, containing PGPR that inhibits the growth of phytopathogenic microorganisms, and (3) phytostimulator, containing PGPR that have ability to produce phytohormones (Vejan et al. [2016\)](#page-30-19). Various agronomically imperative PGPR include the species, such as *Alcaligenes* sp., *Caulobacter*, *Serratia*, *Erwinia*, *Bacillus, Enterobacte*r,*Phyllobacterium* sp., and*Bacillus thuringiensis*, *Hyphomicrobium*, *Azotobacter*, *Azospirillum,* and *Acetobacter* (Sharma et al. [2013;](#page-28-15) Ahemad and Kibret [2014;](#page-20-20) Vejan et al. [2016;](#page-30-19) Kour et al. [2019a;](#page-24-18) Verma et al. [2016a,](#page-29-9) [b\)](#page-29-10). The PGPR used as bio-pesticides and biofertilizers for supportable farming have augmented enormously all over the world. The useful properties of PGPR on the improvement and the production of crops have been studied and reported by worldwide on a wide variety of crops such as pulses, vegetables, cereals, and oilseed crops (Gouda et al. [2018\)](#page-23-22). Numerous PGPRs belonging to genera *Pseudomonas*, *Bacillus*, *Azospirillum,* and *Enterobacter* have been screened from the rhizospheric habitat of various economically important crops and were reported for their synergistic effect on plant growth promotion (Egamberdiyeva et al. [2001\)](#page-22-21).

# **11.8 Conclusions and Future Prospects**

Halophilic microbes are isolated from saline soils or rhizosphere of halophytic plants and shows plant growth-promoting characters directly like the production of IAA, solubilization of phosphate, production of siderophore, fixation of  $N_2$ , deaminase ACC activity, or indirect ways by controlling phytopathogens under saline condition. However, the habitats of halophilic microbes may be rhizosphere, endophytic, or phyllosphere, and these microbes can augment the biomass and productivity of crops using the halophytic and halotolerant crops. The inoculation of halotolerant microbes in the rhizosphere of crops is a viable strategy for eco-friendly approach and supportable improvement of crop in salt-related farming, which consist of cultivation of crops in dry and semidry regions. Several possibilities of study would move us earlier to accepting these approaches for salt-related cultivation. Knowledge of plant–microbe interactions facilitates policies for the protection of crops and saline soil remediation, and this type of interactions is also observed in the area for ecological appreciative of microbes, which promotes halophyte to adaptability in salinity-rich environment.

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