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Ajar Nath Yadav
Joginder Singh
Chhatarpal Singh
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14 Mitigation Strategies for Abiotic Stress Tolerance in Plants Through Stress-Tolerant Plant Growth-Promoting Microbes

Salma Mukhtar, Kauser Abdulla Malik, Samina Mehnaz, and Zabish Khaliq

Abstract

Crop production is adversely affected by a number of abiotic stresses that arise due to anthropogenic activities and inherent edaphic factors. Several agronomic strategies have been used to mitigate the abiotic stresses to increase crop yield. Recently, researchers have been intrigued by the rhizosphere associated microorganisms from the plants growing in extreme environments. Bacterial strains belonging to the phyla Proteobacteria, Actinobacteria, Firmicutes, and archaeal strains related to the phyla Crenarchaeota and Euryarchaeota were abundantly found in the rhizosphere of plants growing under abiotic stress conditions. The well-known PGP strains include *Bacillus, Rhizobium, Frankia, Azotobacter, Azospirillum, Paenibacillus, Serratia, Pseudomonas,* and *Klebsiella*. Plant associated microbial communities promote plant growth under extreme conditions by mineral solubilization, phytohormones production, nitrogen fixation, siderophore, and HCN production. A number of rhizobacterial and archaeal strains have the ability to enhance plant defense mechanisms against different bacterial and fungal pathogens by the production of different antibacterial and antifungal compounds. Meta-omics approaches including metagenomics, metatranscriptomics, and metaproteomics are commonly used for microbial diversity analysis and microbe-mediated stress alleviation in different crops growing under extreme conditions. This chapter gives an overview of the archaeal and bacterial diversity

S. Mukhtar (✉)
School of Life Sciences, Forman Christian College (A Chartered University), Lahore, Pakistan

School of Biological Sciences, University of the Punjab, Lahore, Pakistan

K. A. Malik · S. Mehnaz · Z. Khaliq
School of Life Sciences, Forman Christian College (A Chartered University), Lahore, Pakistan

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residing in the rhizosphere and root endosphere of plants growing under extreme environments and also explained different microbe-mediated mitigation strategies in plants under various abiotic stresses.

Keywords

Biofertilizers · Extreme environments · Meta-omics · Plant–microbe interactions · Rhizosphere microbiome

14.1 Introduction

Agricultural land is adversely affected due to various abiotic stresses such as drought, salinity, acidity, alkalinity, low/high temperatures, and nutrient starvation and this ultimately affects the crop production (Onaga and Wydra 2016; Pareek et al. 2009). More than 60% of the area is affected by drought globally, about 6% of the global land has been affected by salinity, 15% by acidic soils, 9% by minerals deficiency, and 57% by cold environments (Bui 2013; Cramer et al. 2011; Mittler 2006). In different regions of the world, about 30–70% plant growth is affected by abiotic or biotic stresses. Water uptake, biochemical, and physiological processes of plants were affected and production of major crops such as wheat, rice, maize, and sugarcane is reduced and ultimately a threat to global food security is potentially increasing (El-Beltagy and Madkour 2012; Mahalingam 2015; Tigchelaar et al. 2018).

Plants growing in extreme environments have adapted different protective, physiological, and genetic strategies to deal with adverse environmental conditions (Yolcu et al. 2016; Verma et al. 2019). A number of chemical compounds known as plant growth regulators produced by plants are usually used to modulate plant growth under different abiotic and biotic stresses (Vineeth et al. 2016; Wakchaure et al. 2018; Zhao et al. 2009). Plant hormones such as auxins, cytokinins, gibberellins, abscisic acid, and salicylic acid are considered as important growth regulators that control plant growth by playing an important role in plant metabolism and ultimately mitigation of abiotic stresses (Hu et al. 2013; Kazan 2013; Teale et al. 2006; Sharaff et al. 2020). The level of phytohormone production may be changed with the increase in abiotic stresses that adversely affect plant growth (Debez et al. 2001; Khan et al. 2014). Some synthetic compounds, for example, thiourea can be used as a plant growth regulator which promotes growth and productivity, particularly under extreme environments (Garg et al. 2006; Iqbal and Ashraf 2013; Islam et al. 2016).

Microbial communities associated with the plants growing under extreme conditions play a vital role in plant growth by increasing the nutrients available to the plants, help to tolerate abiotic stresses and provide resistance against different plant pathogens (Bulgarelli et al. 2012; Liljeqvist et al. 2015; Sessitsch et al. 2012; Turner et al. 2013; Yadav 2017). Extremophilic microorganisms including xerophiles, halophiles, acidophiles, alkaliphiles, and thermophiles have a genetic and physiological modification to survive under extreme conditions (Mukhtar et al. 2018a; Souza et al. 2015). Plant growth-promoting microbes enhance plant growth by increasing the nutrient availability to the plants such as nitrogen (N), potassium (K), phosphorus (P), and zinc (Zn), nitrogen fixation, production of phytohormones, including auxins, cytokinins, gibberellins, abscisic acid, and salicylic acid, production of siderophores and hydrogen cyanide (HCN) (Mukhtar et al. 2017; Yadav et al. 2017a; Yadav et al. 2020e, f). Root-associated bacteria and archaea also produce a variety of antifungal and antibacterial compounds that can be used to control various fungal and bacterial plant diseases (Jaisingh et al. 2016; Kumar et al. 2011; Subrahmanyam et al. 2020). Plant microbiome also improves plant health by suppressing bacterial and fungal pathogens such as *Xanthomonas* sp., *Fusarium* sp., *Aspergillus flavus,* and *Alternaria* sp. (Mehnaz et al. 2010; Khan et al. 2018; Singh et al. 2020a).

With the progress in the next sequencing approaches, interest in the microbial diversity analysis from the rhizosphere of plants growing under extreme environments has been increased (Mukhtar et al. 2018c, 2019a, b; Naik et al. 2009). Meta-omics approaches such as metagenomics, metatranscriptomics, and metaproteomics help us to understand the functional characterization of plant-associated microbial communities from extreme environments (Venter et al. 2004; Wilmes and Bond 2006; Zeyaullah et al. 2009; Zhou et al. 2015). These techniques can also be used to study the potential of plant growth-promoting bacteria and their role in the mitigation of abiotic stresses under various extreme environments (Castro et al. 2013; Liu et al. 2015; Wang et al. 2016). In this chapter, we have discussed the plant-associated microbial communities from various extreme environments and their role in growth promotion of economically important crops grown in areas that are affected by abiotic stresses.

14.2 Microbial Diversity of Microbes of Plants Growing Under Extreme Environments

The plant microbiome can be classified according to plant parts, such as rhizosphere, phyllosphere, and endosphere microbiomes (Fig. 14.1). The plant microbiome plays an important role in plant health and productivity. Rhizosphere and root endospheric bacteria, archaea, and fungi enable host plants to survive under extreme conditions (Hashem et al. 2016; Mukhtar et al. 2018b, c; Verma et al. 2014). Rhizosphere associated microbial communities have the ability to carry out metabolic processes that improve the soil health and promote the plant growth under abiotic stresses (Egamberdieva 2009; Khan et al. 2014; Biswas et al. 2018). Plant growth-promoting microorganisms can directly enhance plant health and productivity through mineral solubilization, fixation of atmospheric nitrogen, and production of phytohormones (Browne et al. 2009; Mehnaz et al. 2010; Mukhtar et al. 2019e). Some PGP microorganisms produce antibacterial and antifungal compounds, such as siderophores, HCN, and triazole to protect plants against different bacterial and fungal pathogens under extreme conditions. These microbes also trigger plant

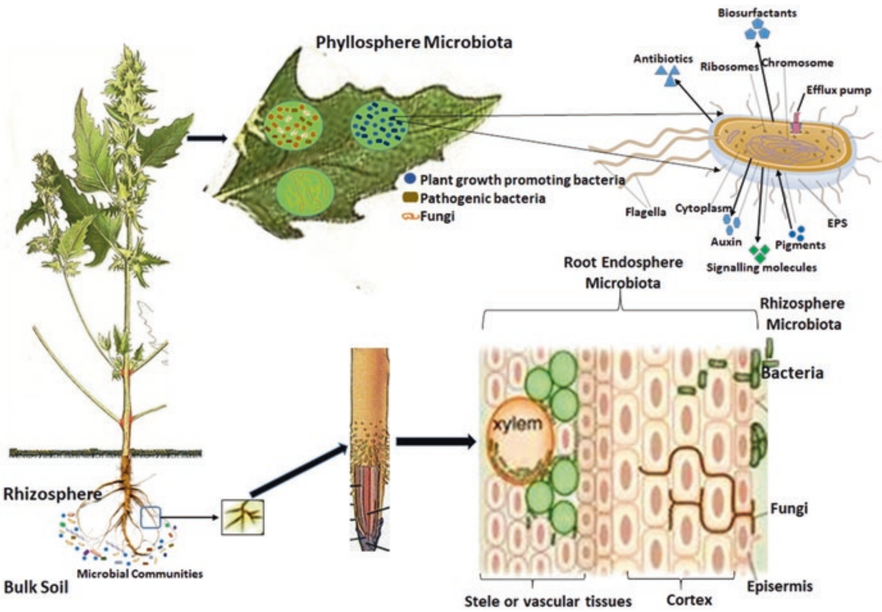

Fig. 14.1 Overview of the halophilic microbiome, their functions, and impact of microbial communities in the rhizosphere, endosphere, and phyllosphere of halophytes, Adapted from Mukhtar et al. (2019b)

immunity and increase resistance against pathogens (Khan et al. 2017; Mehnaz et al. 2010; Mukhtar et al. 2019e).

14.2.1 Saline Environments

Abiotic factors, including soil salinity and drought, are affecting the plant's growth and decreases crop yield by more than 40% and it increases day by day (Pitman and Lauchl 2002). At least 0.2 M NaCl is required for the growth of halophilic microorganisms from the hypersaline environments. Based on different salt concentrations, halophiles are classified as slight, moderate, and extreme halophiles. About 0.2–0.9 M NaCl concentrations are required for slight halophiles growth, 0.9–3.4 M NaCl concentrations are required for moderate halophiles growth, and 3.4–5.2 M NaCl concentrations are required for the optimal growth of extremophilic halophiles (DasSarma and DasSarma 2015; Mukhtar et al. 2018a). Halophiles have tolerance for different salt concentrations and can grow in various saline environments (Yadav et al. 2020a). Different parameters, such as pH, salt concentration, nutrients, and temperature variations affect the physiology of halophiles (Ruppel and FrankenP 2013). Halophilic bacteria and archaea use two main strategies to tolerate high osmotic stress. Mostly halophilic archaea and methanogenic bacteria use "Salt in" strategy. They acquire high KCl ions concentration copes with the high salt stress environment. Halotolerant and halophilic bacteria have the ability to grow in salt-affected environments by using small organic molecules, such as betaine, proline, ectoine, glutamine, and trehalose (DasSarma and DasSarma 2015; Oren 2015). Plant growth-promoting halophilic bacteria and archaea have also the ability to increase plant salt tolerance (Yadav et al. 2019; Yadav et al. 2017b). Halotolerant and halophilic bacterial genera including *Pseudomonas*, *Halomonas, Micrococcus, Planococcus, Marinococcus, Halobacillus, Virgibacillus, Arthrobacter, Nesterenkonia, Brachybacterium, Brevibacillus,* and *Pantoea* have been isolated from the rhizosphere of different halophytes as shown in Fig. 14.2 and Table 14.1 (Meng et al. 2018; Rueda-Puente et al. 2010; Zhao et al. 2016; Yadav et al. 2015d). Growth of barley and oat was increased in salinity environment by inoculation of *Pseudomonas* and *Bacillus* strains (Chang et al. 2014; Orhan 2016; Roy et al. 2014). *Burkholderia* strain PsN also positively affects the salt stress and increase maize growth (Naveed et al. 2014). *Halobacillus* and *Halomonas* were reported to increase of wheat growth and *Streptomyces* strain for tomato growth under salinity-affected environments (Palaniyandi et al. 2014). Soil and roots of halophytes, such as *Sporobolus, Dichanthium, Suaeda, and Cenchrus* have been used for the isolation and characterization of halophilic archaeal strains. Haloarchaeal strains such as *Halococcus, Halobacterium, Haloarcula,* and *Haloferax* have been studied for their plant growth-promoting abilities under hypersaline conditions (Wang et al. 2009; Yadav et al. 2015d) (Fig. 14.3 and Table 14.1).

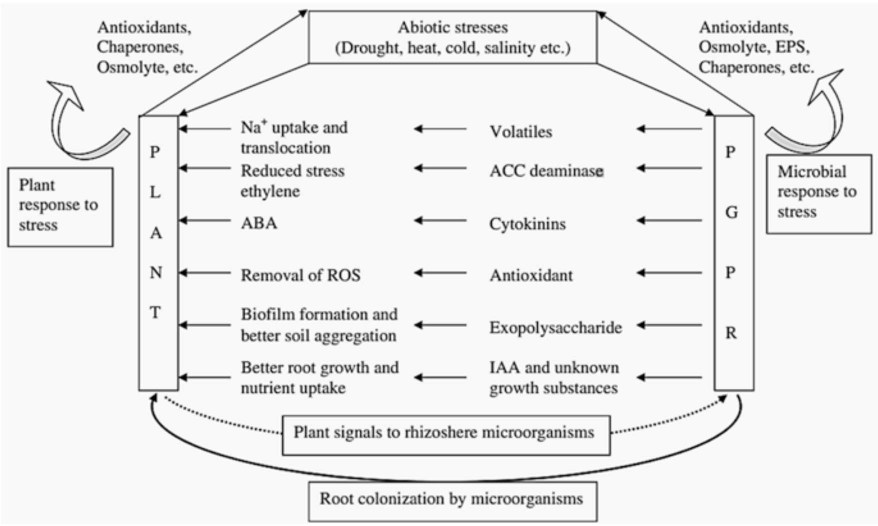

Fig. 14.2 A Conceptual diagram on the plant–microbe interactions under abiotic stress. Adapted from Grover et al. (2011)

Table 14.1 Plant growth-promoting microorganisms from different extreme environments

Extreme habitats/ microbe	PGP attributes	Host–plants	Reference
Salinity			
Virgibacillus	P-solubilization and siderophore production	*Acacia* spp.	Yadav et al. (2015e)
Halomonas	IAA production and ACC deaminase activity	*Salicornia bigelovii*	Rueda-Puente et al. (2010)
Marinococcus	P-solubilization, IAA production, and nitrogen fixation	*Salicornia* spp.	Mapelli et al. (2013)
Halobacillus	P-solubilization, IAA production, and biocontrol activity	*Salicornia europaea*	Zhao et al. (2016)
Micrococcus	P-solubilization and siderophore production	*Urochloa mutica*	Mukhtar et al. (2016)
Oceanobacillus	Mineral solubilization, IAA and siderophore production	*Atriplex amnicola*	Mukhtar et al. (2019a); (Mukhtar et al. 2019d)
Planococcus	P-solubilization and IAA production	*Triticum aestivum*	Rajput et al. (2013)
Pseudomonas	P-solubilization, nitrogen fixation, and siderophore production	*Hordeum vulgare*	Chang et al. (2014)
Salinivibrio	IAA and siderophore production	*Salsola stocksii* and *Atriplex Atriplex leucoclada amnicola*	Mukhtar et al. (2019a); (Mukhtar et al. 2019d)
Arthrobacter	Mineral solubilization, IAA, and siderophore production	*Atriplex leucoclada*	Ullah and Bano (2015)
Nesterenkonia	N_2 fixation, mineral solubilization, IAA, HCN, and siderophore production	*Salicornia strobilacea*	Mapelli et al. (2013)
Brachybacterium	Mineral solubilization and IAA production	*Salicornia brachiata*	Jha et al. (2012)
Pantoea	N_2 fixation, IAA, HCN, and siderophore production	*Suaeda salsa*	Siddikee et al. (2010)
Brevibacillus	Mineral solubilization, IAA, and siderophore production	*Wheat*	Yadav et al. (2018)
Haererohalobacter	Mineral solubilization, IAA, and siderophore production	*Salicornia brachiate*	Gontia et al. (2011)
Lysinibacillus	Mineral solubilization, IAA, and siderophore production	*Prosopis strombulifera*	Sgroy et al. (2009)
Halobacterium	P-solubilization and Nitrogen fixation	*Oryza sativa*	Wang et al. (2009)
Haloferax	IAA production and biocontrol activity	*Suaeda nudiflora*	Saxena et al. (2015)

(continued)

Table 14.1 (continued)

Extreme habitats/ microbe	PGP attributes	Host–plants	Reference
Halococcus	P-solubilization and siderophore production	*Sporobolus indicus*	Yadav et al. (2015d)
Drought			
Bacillus	P-solubilization, ACC deaminase activity, and IAA production	*Cupressus dupreziana*	Jorquera et al. (2012)
Kocuria	P-solubilization, ACC deaminase activity, and nitrogen fixation	*Zygophyllum dumosum*	Steinberger et al. (1995)
Frankia	P-solubilization and nitrogen fixation	*Aristida plumosa*	Bhatnagar and Bhatnagar (2009)
Virgibacillus	P-solubilization, IAA, HCN, and siderophore production	*Triticum aestivum*	Verma et al. (2016)
Azotobacter	P-solubilization, IAA production, and nitrogen fixation	*Artemesia* sp.	Hamdi and Yousef (1979)
Rhizobium	N_2 fixation, IAA and siderophore production	*Psoralea corylifolia*	Sorty et al. (2016)
Enterobacter	P-solubilization, nitrogen fixation, IAA, HCN, and siderophore production	*Phoenix dactylifera*	Ferjani et al. (2015)
Chryseobacterium	Nitrogen fixation, HCN, and siderophore production	*Glycine max*	Dardanelli et al. (2010)
Azoarcus	Nitrogen fixation, IAA, and siderophore production	*Leptochloa fusca*	Malik et al. (1997)
Pantoea	N_2 fixation, IAA, HCN, and siderophore production	*Suaeda salsa*	Siddikee et al. (2010)
Halobacterium	P-solubilization and nitrogen fixation	*Oryza sativa*	Wang et al. (2009)
Halococcus	P-solubilization and siderophore production	*Sporobolus indicus*	Yadav et al. (2015d)
Pseudomonas libanensis	Alleviation of drought stress and plant growth promotion	Wheat, maize, rice, sorghum, and finger millet	Kour et al. (2020b)
Streptomyces laurentii	Microbe-mediated alleviation of drought stress and acquisition of phosphorus in great millet (*Sorghum bicolour* L.)	*Amaranthus*, buckwheat, millets, and maize	Kour et al. (2020a)
Acinetobacter calcoaceticus	Amelioration of drought stress in foxtail millet (Setaria italica L.)	Wheat, maize, foxtail millet, and finger millet	Kour et al. (2020c)
Acidity			
Acidithiobacillus	P-solubilization, IAA, HCN, and siderophore production	*Pinus rigida*	Dang et al. (2017)

(continued)

Table 14.1 (continued)

Extreme habitats/ microbe	PGP attributes	Host–plants	Reference
Methylobacterium	P-solubilization, ACC deaminase activity, IAA, HCN, and siderophore production	*Triticum aestivum*	Wellner et al. (2011)
Lysinibacillus	P-solubilization, IAA, HCN, and siderophore production	*Triticum aestivum*	Verma et al. (2013)
Flavobacterium	P and K solubilization and biocontrol activity	*Hordeum vulgare*	Verma et al. (2014)
Azotobacter	P-solubilization, IAA production, and nitrogen fixation	*Artemesia* sp.	Upadhyay et al. (2009)
Pseudomonas	P-solubilization, IAA, HCN, and siderophore production	*Triticum aestivum*	Verma et al. (2013)
Pyrococcus	P and K solubilization and biocontrol activity	Thermal marine sediments	Gao et al. (2003)
Alkalinity			
Pseudorhodoplanes	IAA production, P-solubilization, and nitrogen fixation	*Photinia fraseri*	Seker et al. (2017)
Sphingomonas	P-solubilization and IAA production	*Smallanthus sonchifolius*	Moraes et al. (2012)
Curtobacterium	IAA production and P-solubilization	*Chrysanthemum morifolium*	Zawadzka et al. (2014)
Kocuria	P-solubilization, IAA production, and nitrogen fixation	*Dichanthium annulatum*	Mukhtar et al. (2018b)
Burkholderia	IAA and ACC deaminase production and nitrogen fixation	*Vitis vinifera*	Barka et al. (2006)
Paenibacillus	IAA production, P-solubilization, and nitrogen fixation	*Photinia fraseri*	Seker et al. (2017)
Heat			
Bacillus	P-solubilization, IAA, and siderophore production	*Triticum aestivum*	(Verma et al. 2018)
Arthrobacter	P-solubilization, IAA, and biocontrol activity	*Triticum aestivum*	Kumar et al. (2011)
Pseudomonas	P and Zn solubilization, IAA, HCN, and siderophore production	*Triticum aestivum*	Vyas et al. (2009)
Providencia	P and Zn solubilization, IAA production, and nitrogen fixation	*Amaranthus viridis*	Forchetti et al. (2007)
Staphylococcus	P-solubilization, HCN, and siderophore production	*Cupressus dupreziana*	Jorquera et al. (2012)

(continued)

Table 14.1 (continued)

Extreme habitats/ microbe	PGP attributes	Host–plants	Reference
Streptomyces	P-solubilization and biocontrol activity	*Vigna unguiculata*	Dimkpa et al. (2008)
Geobacillus	P-solubilization, IAA, and siderophore production and biocontrol activity	Petroleum contaminated Kuwait soil	Zeigler (2014) Al-Hassan et al. (2011)
Halococcus	P-solubilization and siderophore production	*Sporobolus indicus*	Yadav et al. (2015d)
Cold			
Kocuria	P-solubilization, IAA production, and nitrogen fixation	*Triticum aestivum*	Yadav et al. (2015a)
Bacillus	P-solubilization, IAA, and siderophore production	*Capsicum annuum*	Barka et al. (2006)
Arthrobacter	P-solubilization, IAA, and biocontrol activity	*Pinus roxburghii*	Singh et al. (2016)
Klebsiella	P-solubilization, IAA, and siderophore production	*Zea mays*	Rana et al. (2017)
Lysinibacillus	Mineral solubilization, IAA, and siderophore production	*Prosopis strombulifera*	Sgroy et al. (2009)
Pseudomonas	P-solubilization, nitrogen fixation, IAA, HCN, and siderophore production	*Solanum tuberosum*	Sati et al. (2013)
Methanosarcina	P-solubilization, IAA, and siderophore production and biocontrol activity	Siberian permafrost	Morozova and Wagner (2007)
Methylobacterium	P-solubilization, ACC deaminase activity, IAA, HCN, and siderophore production	*Triticum aestivum*	Saxena et al. (2016)

14.2.2 Arid and Semi-Arid Environments

Moisture content of the soil also affects the microbial communities associated with plants growing under arid and semi-arid environments. Moisture content is the main abiotic factor that affects microbial diversity associated with xerophytes, such as *Leptochloafusca, Aristida plumose, Zygophyllum dumosum, Artemesia* sp. and *Cupressus dupreziana* (Bhatnagar and Bhatnagar 2009; Buyanovsky et al. 1982). These microorganisms use small organic solutes, such as sugars, amino acids, and some other organic molecules including glutamine, ectoine, betaine, and trehalose to maintain their internal environment. The rhizosphere microbiome of xerophytes is getting more attention than other soil microbiomes since the last decade, due to its effectiveness (Jorquera et al. 2012). Microbiome of xerophytes has about 54% microbial diversity of Gram-positive bacteria especially Actinomycetes, such as *Kocuria*, *Streptomyces, Frankia,* and *Micrococcus* (Eppard et al. 1996; Steinberger et al. 1995). Some other genera such as *Azoarcus, Azotobacter, Bacillus, Enterobacter,* and

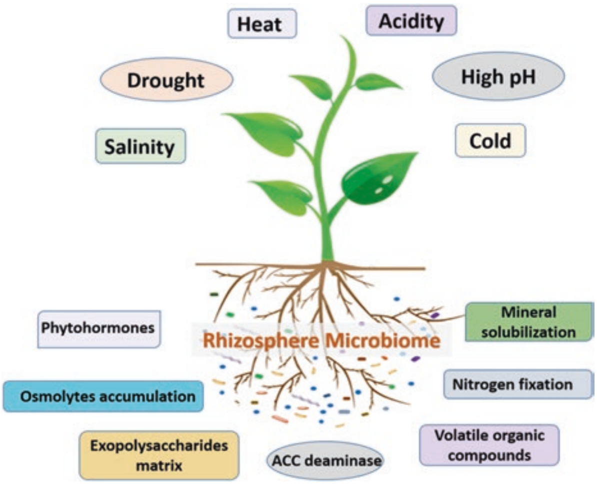

Fig. 14.3 Overview of microbe-mediated mitigation of abiotic stresses by plants. Adapted from Mukhtar et al. (2019c)

Virgibacillus have also been identified from the rhizosphere of xerophytes (Bhatnagar and Bhatnagar 2009; Kour et al. 2017; Malik et al. 1997). *Bacillus licheniformis* strain K11 has been reported to increase the growth of pepper plants in drought stress conditions (Figs. 14.2 and 14.3; Table 14.1). *Kocuria, Bacillus,* and *Pseudomonas* being drought-tolerant bacterial genera also have plant growth-promoting abilities, such as nitrogen fixation, HCN, P-solubilization, IAA, and siderophore production. These bacteria can also be used as bioformulation and biocontrol agents for different crops growing in arid and semi-arid environments (Jorquera et al. 2012; Kour et al. 2017; Lim and Kem 2013; Saxena et al. 2020; Thakur et al. 2020).

14.2.3 Acidic Environments

Soil pH plays an important role in shaping the composition of microbial communities associated with plants growing in acidic or alkaline environments (Feliatra et al. 2016; Wellner et al. 2011). Rhizosphere is the most active site for microbial diversity analysis from acidic environments. Many acidophilic and acidotolerant bacteria and archaea including *Pseudomonas, Azotobacter, Lysinibacillus, Acidithiobacillus, Serratia, Flavobacterium,* and *Pyrococcus* have been isolated and characterized from the various acidic environments (Dang et al. 2017; Feliatra et al. 2016; Upadhyay et al. 2009; Wellner et al. 2011). These microorganisms stimulate plants to withstand extremely acidic conditions and maintain their internal pH (Figs. 14.2 and 14.3; Table 14.1). Many PGP bacterial strains identified from the acidophilic environments promote plant growth of various crops such as rice, wheat, maize, and sugarcane to grow under acidic conditions (Verma et al. 2013; Wellner et al. 2011). Acidophilic microorganisms produce siderophores that are important for their survival under acidic conditions. These microbes have the ability to convert Fe^{3+} to Fe^{2+} in an acidic environment (Sorty et al. 2016; Vansuyt et al. 2007). Acid-tolerant microorganisms have been used as bio-inoculants for crops growing under acid-affected soil.

14.2.4 Alkaline Environments

Microbial diversity of different soda lakes around the world have been studied extensively during the last decade. The pH range of soda lake water is usually from 8 to 10 and even sometimes more than 12 (Antony et al. 2013; Grant and Sorokin 2011). The rhizosphere of plants such as *Dichanthium annulatum, Chrysanthemum morifolium, Photinia fraseri,* and *Smallanthus sonchifolius* present in the alkaline environment has unique microbial diversity as compared to soils with neutral pH because alkaline soils have less carbon and more methane and hydrogen content (Pikuta et al. 2003; Tiago et al. 2004). These microorganisms maintain their functional and structural integrity of cytoplasmic proteins by using specific proteins and enzymes (Jones et al. 1998; Zawadzka et al. 2014). Many alkaliphilic bacterial and archaeal strains such as *Sphingomonas, Pseudorhodoplanes*, *Paenibacillus, Arthrobacter, Burkholderia,* and *Curtobacterium* have been characterized by alkaline environments (Figs. 14.2 and 14.3; Table 14.1). A huge number of microbes identified from alkaline environments showed phytohormones production and P-solubilization ability (Rastegari et al. 2020; Yadav 2020). Rhizosphere microbiome of crops such as wheat, rice, maize, and barley are considered as important sources for maintaining the production and yield of these crops. These alkaliphilic bacteria having multi PGP abilities can be used for the improvement of plant growth in alkaline environments (Mukhtar et al. 2018b; Nautiyal et al. 2000).

14.2.5 Hot Environments

Temperature is one of the important abiotic factors which has effects on seed germination, photosynthesis rate, and membrane permeability of plants (Xu et al. 2014). Various plants growing in hot environments such as *Triticum aestivum, Vigna unguiculata, C. dupreziana,* and *Sporobolus indicus* have special enzymes and proteins to survive under hot environments. Rhizosphere and root-associated microbial communities from these environments have the ability to promote plant growth by increasing phytohormones production, nitrogen fixation, HCN and siderophores production, and P-solubilization as shown in Fig. 14.2 and Table 14.1 (Mukhtar et al. 2017; Vyas et al. 2009; Verma et al. 2018). Many bacteria have the ability to solubilize different minerals such as P, Zn, Al, and K by producing different organic acids, gluconic acid, formic acid, and citric acid in high temperature (Verma et al. 2014, 2016). A huge number of microbial genera such as *Staphylococcus, Arthrobacter, Streptomyces, Pseudomonas, Providencia,* and *Geobacillus* could be used as biofertilizers for plants growth under hot environments (Dimkpa et al. 2008; Gao et al. 2003; Zeigler 2014).

14.2.6 Cold Environments

Microbial diversity from cold environments is of particular importance in global ecology. A number of lakes and other aquatic ecosystems have very low temperatures permanently or seasonally (Singh 2014; Yadav et al. 2015b; Yadav et al. 2015c). Some plant species such as *Pinus roxburghii, Zea mays, Capsicum annuum,* and *T. aestivum* can grow under cold conditions by freezing tolerance or avoiding cooling of the tissue water (Thomashow 2010). Psychrophilic microorganisms have maximum functional activities at low temperatures as compared to mesophiles. Cold-tolerant plants have different microbial diversity and ability to tolerate cold and drought stress by solubilization of minerals, activation of defense-related and cold-active enzymes, production of phytohormones and exopolysaccharides (Ait Bakra et al. 2006; Kaushal and Wani 2016; Yadav et al. 2016) (Figs. 14.2 and 14.3; Table 14.1).

Many cold-tolerant bacterial strains including *Bacillus, Kocuria, Arthrobacter, Janthinobacterium, Klebsiella, Lysinibacillus, Paenibacillus, Providencia, Methylobacterium,* and *Methanosarcina* were characterized from cold-tolerant plants (Selvakumar et al. 2011; Shukla et al. 2016; Singh 2014; Singh et al. 2016; Yadav et al. 2015a). A number of endophytic cold-tolerant bacterial strains were isolated from crops growing under the low-temperature conditions (Rana et al. 2020). These bacterial strains showed the ability to solubilize minerals, produce phytohormones, siderophores, and HCN (Rana et al. 2017). Psychrophilic plant growth microorganisms can be used as biofertilizers for improvement of crops such as wheat, rice, and sugarcane growing under cold environments (Kour et al. 2020a; Kour et al. 2020b; Kour et al. 2020c; Kour et al. 2020d).

14.3 Mitigation Strategies for Abiotic Stress Tolerance in Plants

14.3.1 Phytohormones Production

Among the production of many plant beneficial chemicals, the production of phytohormones, such as auxins, cytokinins, gibberellins, ethylene, and abscisic acid, is key striking aspects of extremophilic bacteria imparting plant growth promotion under the unsuitable salt-affected area (Dodd and Perez-Alfocea 2012). The cellular mechanisms of plant growth promotion along with increased root length, due to IAA producing PGPR are direct stimulation of cell differentiation and division (Desale et al. 2014; Gonzalez et al. 2015; Shakirova 2007; Trindade et al. 2010; Tiwari et al. 2020). The genera of halophilic/tolerant bacteria described as PGPRs are *Bacillus, Enterobacter, Micrococcus, Pseudomonas, and Serratia*. These bacteria, when used as inoculants for the host plants, showed improved growth of wheat, sugarcane, and corn, improved catalase and peroxidase activity along with the increased level of TSS (total soluble sugar) content, some amino acids and K+/ Na + ratio under salt stress (Gontia et al. 2011; Mukhtar et al. 2017a, b; Mukhtar et al. 2019d). Cytokinins, the plant growth-stimulating phytohormone, are revealed to be produced by hypersaline soil isolated *Halobacillus* strain which increased shoot biomass under salt stress (Figs. 14.3 and 14.4; Table 14.1). The cytokinins signaling is not one-way signaling mechanism as shown by many studies, cytokinins producing *Bacilli* increased shoot biomass but reduced root length which may be due to the presence of abscisic acid in the roots (Arkhipova et al. 2007; Ilangumaran and Smith 2017). Some plant-associated methylotrophs, such as *Methylobacterium* and *Methylovorusmays,* synthesize and excrete indole acetic acid and cytokinins (Ivanova et al. 2001).

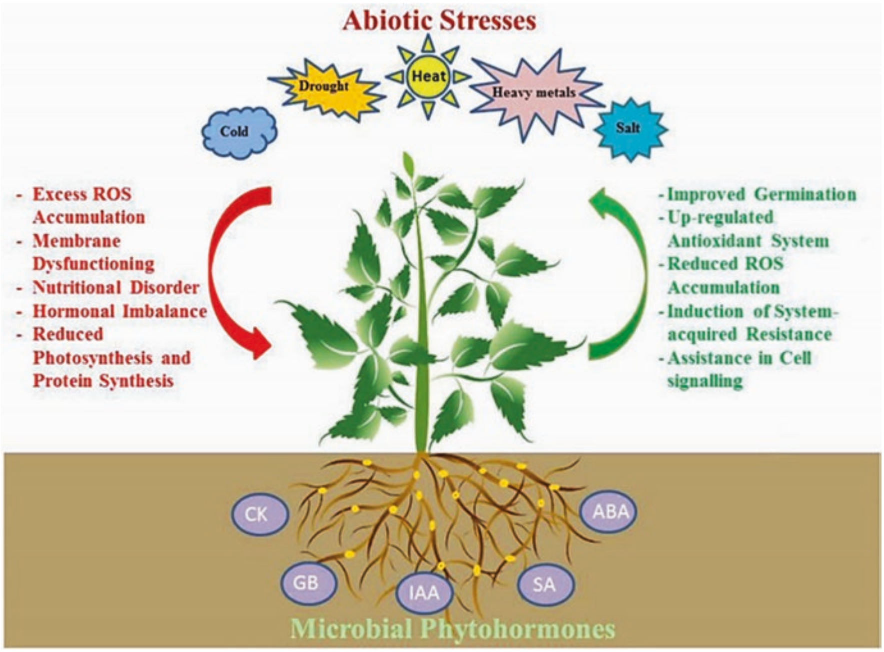

Fig. 14.4 An overview of mechanisms in microbial phytohormone-mediated plant stress tolerance. Rhizosphere-associated microorganisms produce indole-3-acetic acid (IAA), cytokinin (CK), gibberellin (GB), abscisic acid (ABA), and salicylic acid (SA) that help plants to withstand stress by enhancing its antioxidant potential, by upregulation of the antioxidant system and by the accumulation of compatible osmolytes thus reducing oxidative stress-induced damage; improving photosynthetic capacity and membrane stability; promoting cell division and stomatal regulation; stimulating the growth of root system, and acquisition of water and nutrients. Adapted from Egamberdieva et al. (2017)

14.3.2 Nitrogen Fixation

Nitrogen fixation by microbes is considered as one of the major methods for plant growth promotion because these microbes have the ability to fix atmospheric nitrogen and change it to nitrate that requires for the healthy and enhanced plant growth (Glick 2012; Kour et al. 2020d; Kaur et al. 2020). Frequently documented bacterial nitrogen-fixing genera include *Azotobacter, Azospirillum, Frankia, Bacillus, Klebsiella, Paenibacillus, Pantoea, Pseudomonas, Rhizobium, Salinibacter, and Serratia* (Ahmad and Kebret 2014; Jaisingh et al. 2016; Kuan et al. 2016). Apart from atmospheric nitrogen fixation, most of the plant growth-promoting rhizobacteria, root endophytic bacteria, as well as archaea, can produce phytopathogen (bacterial or fungal) limiting compounds to be used for biocontrol (Jaisingh et al. 2016; Kumar et al. 2011; Mondal et al. 2020). Rhizosphere microbiome was recognized as a source of suppressing fungal phytopathogens like, *Alternaria* sp., *Aspergillus flavus*, and *Fusarium* sp. making plants resistant to tested pathogens (Mehnaz et al. 2010). Plants from extreme environments have been explored to exploit associated microbiomes and several studies reported successful isolation and use of these isolates for the plant growth promotion. Such N_2-fixing reported genera are *Azospirillum* (Omar et al. 2009), *Bacillus* (Mukhtar et al. 2018a; Sorty and Shaikh 2015; Sorty et al. 2016)*, Bradyrhizobium* (Panlada et al. 2013; Swaine et al. 2007), *Burkholderia* (Barka et al. 2006), *Enterobacter* and *Klebsiella* (Sorty et al. 2016; Mukhtar et al. 2017a, b), *Frankia* (Tani et al. 2003), *Micrococcus* (Dastager et al. 2010; Oliveira et al. 2009; Steinberger et al. 1995), *Pseudomonas* (Ali et al. 2009; Grichko and Glick 2001), *Rhizobium* (Remans et al. 2008; Sorty et al. 2016) with successful plant growth promotion (Figs. 14.2 and 14.3; Table 14.1).

14.3.2.1 Mineral Solubilization

Extremophilic microbes used as PGPR can directly enhance plant nutrient uptake by the roots (Figs. 14.2 and 14.3; Table 14.1). Apart from nitrogen-fixing microbe, many PGPR genera, including *Bacillus, Halobacillus, Enterobacter, Micrococcus, Pseudomonas, Virgibacillus, Pantoea*, *Rhizobium,* and *Serratia* have been reported for the solubilization of minerals (P, K, Zn) along with plant growth promotion (Mukhtar et al. 2017a, b; Sgroy et al. 2009; Yadav et al. 2020b, c). In the case of phosphate, PGPR converts its inorganic form into bioavailable organic phosphates and they can be used as a biofertilizer for the cultivation of barley, sugarcane, maize, rice, and wheat (Farrar et al. 2014; Jaisingh et al. 2016; Mukhtar et al. 2019d; Siddikee et al. 2010). The underlying mechanism for phosphate solubilization by microbes is their ability to produce organic acids; acetic acid, oxalic acid, lactic acid, and citric acid, responsible for phosphate conversion and the reported genera of phosphate solubilizing bacteria are *Bacillus, Enterobacter,* and *Pseudomonas* (Berendsen et al. 2012; Kumar et al. 2011; Ramaekers et al. 2010). The mineral-solubilizing and mobilizing microbes play important role in plant growth promotion, nutrient uptake, and soil health for sustainable agriculture (Kumar et al. 2019; Kumar et al. 2017; Singh et al. 2020b).

Potassium is the third most essential nutrient for plant growth; therefore, potassium solubilizing bacteria are used as biofertilizers in potassium limiting soils for agriculture. The reported PGPR genera for potassium solubilization are *Bacillus, Acidothiobacillus, Paenibacillus, Azospirillum, Marinococcus, Serratia, Streptomyces,* and *Azotobacter* (Zhao et al. 2016; Rana et al. 2019; Verma et al. 2017a, b). Several studies have reported potassium-solubilizing bacteria as biofertilizers for the cultivation of wheat, rice, maize, and sugarcane, to reduce the use of potassium fertilizer (Badar et al. 2006; Etesami et al. 2017). Zinc solubilizing bacteria, isolated from extreme saline environments, showed the ability to convert its inorganic form to organic form for plant uptake and utilization. The reported genera of zinc solubilization from various extreme environments include *Bacillus*, *Pseudomonas, Burkholderia, Brevibacillus,* and *Gluconacetobacter* (Figs. 14.2 and 14.3; Table 14.1) (Desai et al. 2012). These strains possess potentials to be used as chemo-attractants for the plant roots as well as PGPR for enhanced growth (Singh et al. 2020a; Singh and Yadav 2020; Yadav et al. 2020d).

14.3.2.2 ACC Deaminase Production

ACC deaminases, a viral compound for helping plants grow in unsupportive environmental conditions. Many rhizobacteria including *Oceanobacillus, Bacillus, Achromobacter, Halobacillus, Micrococcus, Virgibacillus,* and *Planococcus* can produce ACC deaminase for lowering the amount of ethylene (Figs. 14.2 and 14.3; Table 14.1). Ethylene is a two-step production and enzymatic conversion system; ACC synthase converts AdoMet (*S-adenosylmethionine*) to ACC (1-aminocyclopro pane-1-carboxylic acid), and ACC is converted to ethylene with the help of ACC oxidase (Etesami et al. 2015; Glick, 2014; Nadeem et al. 2007). The ACC deaminase producing plant-associated microbes protect against many abiotic stresses such as salinity, drought, heavy metal, water-logging, and petroleum exposure. ACC deaminase-producing rhizobacteria act as bioprotectant for maintaining ACC levels inside the host plant and its surroundings by hydrolyzing ACC through deaminase. It is indirectly involved in root elongation by lowering the inhibitory effects of ethylene on plant roots (Lima et al. 2011; Nikolic et al. 2011; Yadav et al. 2020g).

14.3.2.3 Exopolysaccharides Matrix

The production of EPS (exo-polysaccharides) by extremophilic rhizobacteria includes *Halobacillus, Pseudomonas, Corynebacterium, Nesterenkonia, Acinetobacter*, and *Planococcus*, works by creating a matrix for attachment of soil particles to plant roots and associated microbes thereafter creating a complex network in the soil within the plant root vicinity. The formation of such complex plant microbe-associated meshwork around the roots helps in establishing successful plant-microbe interactions and imparting bioprotection against phytopathogens such as protest, fungal, and bacterial (Mapelli et al. 2013; Sorty et al. 2016). Apart from providing biological benefits, the production of EPS supports beneficial physical properties of soil, such as water-holding capacity along with stabilizing the soil structure (Figs. 14.2 and 14.3; Table 14.1). Halotolerant PGPR with the ability of

EPS production has been successfully used under arid and saline conditions for chickpea, maize, sugarcane, and wheat (Mukhtar et al. 2019d; Oren 2015).

14.3.2.4 Siderophores Production and Biocontrol

Iron is considered one of the most crucial elements for the plant's growth. It is involved in many plant growth essential mechanisms such as nitrogen fixation, respiration, and photosynthesis (Figs. 14.2 and 14.3; Table 14.1). Iron availability for plant decreased in sodic, saline, arid, and acidic soils hindering healthy plant growth (Abbas et al. 2015). Many PGPR has the ability to produce siderophores which help in iron chelation thus, helping in iron availability for plants (Kour et al. 2019a, b). Production of siderophores by PGPR indirectly provides biocontrol to host plants, many PGPRs such as *Halobacillus, Bacillus, Pseudomonas, Halovibrio, Klebsiella,* and *Rhizobium* isolated from the arid and saline environments have the ability to produce siderophores (Singh et al. 2015).

The most fascinating aspect of PGPRs is the production of antifungal and antibacterial compounds; HCN (hydrogen cyanide), 2,4-diacetylphloroglucinol, pyoluteorin, gliotoxin, pyrrol-nitrin, and tensin. The reported extremotolerant PGPRs genera for antipathogenic compounds include *Aeromonas, Rhizobium, Bacillus, Halomonas, Acinetobacter, Pseudomonas,* and *Enterobacter* (Bhattacharyya and Jha 2012; Singh et al. 2015). The application of these bacteria has successfully protected the plants against tested fungal and bacterial pathogens. Hydrogen cyanide (HCN) is one of the most frequently reported antifungal compounds and has been reported in a number of PGPRs isolated from diversified environments (Barea et al. 2005). Apart from imparting antifungal protection, HCN-producing PGPRs have been reported for mineral (Zn, P, K) mobilization in soils (Frey et al. 2010; Rai et al. 2020; Suman et al. 2016). Some studies have shown that HCN-producing PGPRs in acidic soils play a vital role in iron sequestration, phosphate mobilization, thus increasing the bioavailability of phosphate for the host plants (Ström et al. 2002).

14.4 Conclusion and Future Prospects

Food production has increased as the world population doubled during the last few decades. Plants growing under harsh environments have special genetic and physiological modifications. Microbe-mediated stress alleviations have been extensively studied during the last few years. PGP microorganisms isolated and characterized from the rhizosphere and roots of plants growing under extreme environments can be used as bio-inoculants for increasing crop production under various abiotic stresses. A number of bacterial, archaeal, and fungal strains have the potential to be used as biocontrol agents against different bacterial and fungal diseases. Microbe-mediated abiotic stresses alleviation in crops may also be involved in the production of different organic compounds, especially extracellular enzymes, and can be used to improve soil properties, promote plant growth, and provide as signaling molecules to the plants. By using meta-omics approaches, plant growth-promoting microorganisms can be studied and utilized in a better way for crop improvement and production under abiotic stresses. New information from metagenomics, metatranscriptomics, and metaproteomics will help us to find out new roles of plant-associated microorganisms under extreme environments. Different microbial osmoregulatory and other stress-tolerant genes identified from a number of extreme environments may be used for the development of stress-tolerant transgenic crops in the future.

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