



REVIEW

Microbial diversity in the rhizosphere of plants growing under extreme environments and its impact on crop improvement

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Received: 7 April 2019 / Revised: 24 May 2019 / Accepted: 27 May 2019
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Abstract

Abiotic stresses have adverse effects on the plant growth and productivity. Over the last decades, scientists have been intrigued by the fascinating microorganisms that exist in the rhizosphere of plants growing under extreme environments. Members of bacterial phyla Actinobacteria, Proteobacteria, Firmicutes and Bacteroidetes and archaeal phyla Euryarchaeota and Crenarchaeota are found to be more abundant in the rhizosphere of plants growing in extreme environments. Rhizosphere microbiomes enhance plant growth under abiotic stresses by nitrogen fixation, phytohormones production, mineral solubilization, siderophores and HCN production and eliciting plant defense mechanisms against different bacterial and fungal pathogens. Meta-omics techniques such as metagenomics, metatranscriptomics and metaproteomics can also be used to study complex processes involved in microbe-mediated stress alleviation in different plants growing in extreme environments. These approaches generate multi-layered information that can lead to massive outcomes; hence, there are more chances for implementation in this field. This review summarizes the information about the archaeal and bacterial diversity living in the root microbiome of plants growing under extreme conditions. We also described different mechanisms about role of plant growth promoting microorganisms under abiotic stresses and highlighted the applications of meta-omics approaches to explain further advancement in plant–microbe interactions.

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

Introduction

Abiotic stresses including salinity, drought, alkalinity, acidity, high/low temperatures and nutrient starvation are the main limiting factors involved in loss of crop yields. About 6% of the global land has been affected by salinity, more than 60% by drought, 15% by acidic soils, 9% by minerals deficiency and 57% by cold environments (Bui 2013; Cramer et al. 2011; Mittler 2006). Globally vast areas have been affected due to various biotic and abiotic factors and ultimately cause a great loss in crop yield and production and soil structure and composition (Bui 2013; Onaga and Wydra 2016).

Plants adapt a wide array of protective mechanisms to deal with adverse environmental conditions (Yolcu et al. 2016). The rhizospheres of plants growing in extreme environments harbor unique microbial communities including halophiles, xerophiles, alkaliphiles, acidophiles and thermophiles. Plant microbiomes play an important role in acquiring nutrients or plant growth, help to tolerate abiotic stresses and provide resistance against different plant pathogens (Turner et al. 2013; Yadav 2017). These microorganisms have special physiological and genetic modifications to exist under harsh environments (Singh 2014). Plant growth promoting (PGP) microorganisms promote plant growth by providing various nutrients such as nitrogen (N), phosphorus (P), potassium (K) (Browne et al. 2009) and phytohormones production such as cytokinins, and auxins (Mukhtar et al. 2017; Susilowati et al. 2015). Microbial nitrogen fixation is considered one of the basic mechanism to promote plant growth and mostly rhizobacteria can fix atmospheric nitrogen into nitrate and help plants to grow healthy (Glick 2012; Susilowati et al. 2015). The well-known N-fixing bacteria include *Rhizobium*, *Frankia*, *Serratia*, *Pseudomonas*, *Azotobacter*, *Azospirillum*, *Paenibacillus*, *Pantoea*,

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Klebsiella, *Salinibacter*, *Halobacillus* etc. (Ahmad and Kebret 2014; Jaisingh et al. 2016; Kuan et al. 2016). Some rhizobacteria and root endophytic bacteria and archaea have ability to produce different antibacterial and antifungal compounds and act as biocontrol agents to control various bacterial and fungal plant diseases (Jaisingh et al. 2016; Kumar et al. 2011). Rhizosphere microbiome also improves plant fitness by suppressing the fungal pathogens such as *Fusarium* sp., *Alternaria* sp. and *Aspergillus flavus* and produce a response to make plants resistant to pathogen attack again (Mehnaz et al. 2010). Plant growth promoting rhizobacteria (PGPR) genera *Bacillus* (Mukhtar et al. 2018a; Sorty et al. 2016), *Rhizobium* (Remans et al. 2008; Sorty et al. 2016), *Bradyrhizobium* (Panlada et al. 2013; Swaine et al. 2007), *Azospirillum* (Omar et al. 2009), *Pseudomonas* (Ali et al. 2009; Grichko and Glick 2001), *Enterobacter* and *Klebsiella* (Sorty et al. 2016; Mukhtar et al. 2017), *Burkholderia* (Barka et al. 2006), *Micrococcus* (Dastager et al. 2010; Oliveira et al. 2009; Steinberger et al. 1995) and *Frankia* (Tani et al. 2003) have been well documented from various extreme environments.

Rhizosphere microbial communities of plants growing in extreme environments, e.g., salinity, drought, alkalinity and acidity have been characterized for their potential biotechnological applications in medicine, industry, agriculture, and bioremediation of polluted environments (Farrar et al. 2014; Mukhtar et al. 2018a). Extremophilic microorganisms have ability to survive at 0.80–4.5 M salt concentrations (halophiles), pH < 4 (Acidophiles), pH > 9 (alkaliphiles), 60–111 °C (thermophiles) and –2 to –20 °C (psychrophiles) (Souza et al. 2015; Yadav et al. 2015b). With the advent of next generation sequencing techniques, interest in unculturable microorganisms from the rhizosphere of plants growing under extreme environments has increased. Functional characterization of rhizosphere microbial communities have been reported from a number of extreme environments by using metagenomics and metaproteomic analyses (Bulgarelli et al. 2012; Mukhtar et al. 2018c). Rhizosphere microbiome analysis from extreme environments enables us to understand potential of microorganisms and their importance in the maintenance of soil structure and composition and plant health and productivity. The main objective of this review is to highlight the rhizosphere microbial communities from extreme environments. Here, we have also discussed the role of archaeal and bacterial diversity in stress mitigation processes of plants.

Rhizosphere microbiomes of plants growing under extreme environments

Halophytes rhizosphere microbiome

Soil salinity is the main abiotic factor that affects the plants' growth under hypersaline environments and decreases crops

yields by more than 40% (Pitman and Lauchl 2002). Halophilic organisms can grow in hypersaline environments which require at least 0.2 M NaCl for their growth. They are usually known as slight, moderate and extreme halophiles according to salt requirements. Slight halophiles are microorganisms which can grow at 0.2–0.85 M NaCl (1–5%) concentrations, moderate halophiles that grow optimally at 0.85–3.4 M NaCl (5–20%) concentrations and the extreme halophilic organisms which can grow at 3.4–5.2 M NaCl (21–31%) concentrations (DasSarma and DasSarma 2015; Mukhtar et al. 2018a). Halophiles grow in salinity affected environments and can tolerate a wide range of salt concentrations. The physiology of the halophiles may be affected by change in NaCl concentration, pH, temperature and availability of nutrients (Ruppel et al. 2013). Salt loving archaea and bacteria have evolved two strategies to deal with high osmotic stress. Most of the bacteria use 'compatible solute strategy' in which they accumulate different organic compounds like proline, ectoine, glycine betaine and glutamine. Halophilic archaea and anaerobic bacteria cope with high salt stress by 'salt in strategy' in which they maintain their internal environment by accumulation high concentration of KCl ions (DasSarma and DasSarma 2015; Oren 2015).

Along with many other approaches, plant growth promoting bacteria have also been used to enhance plant salt tolerance (Table 1; Fig. 1). Dominant halophilic and halotolerant bacterial genera including *Halobacillus*, *Halomonas*, *Virgibacillus*, *Micrococcus*, *Marinococcus*, *Pseudomonas* and *Planococcus* have been studied from the rhizosphere of different halophytes as shown in Table 1 (Rueda-Puente et al. 2010; Zhao et al. 2016). *Pseudomonas* and *Bacillus* strains were used to enhance growth of barely and oat in salt stress environments (Mapelli et al. 2013; Chang et al. 2014). *Burkholderia* strain PsN has been reported to enhance salt stress in maize (Naveed et al. 2014), *Streptomyces* sp. strain PGPA39 was described for plant growth promotion of tomato (Palaniyandi et al. 2014) and *Halobacillus* and *Halomonas* are used to enhance wheat growth under salt stress (Orhan 2016). Some halophilic archaeal strains have also been identified from the roots and soils of halophytes, such as *Cenchrus*, *Dichanthium*, *Suaeda* and *Sporobolus* (Table 1). A number of haloarchaeal strains have been characterized for their plant beneficial abilities, such as *Halobacterium*, *Haloferax*, and *Halococcus* (Wang et al. 2009; Yadav et al. 2015b).

Xerophytes rhizosphere microbiome

Abiotic stresses such as moisture, temperature and availability of nutrients affect microbial diversity in desert soils (Fig. 1). The moisture content is the main limiting factor that affects the microbial communities associated with xerophytes such as *Aristida plumose*, *Artemisia* sp., *Cupressus*

Table 1 Plant growth promoting microorganisms from different extreme environments

Abiotic stress	Microorganisms	PGP-attributes	Host-plants	References
Salinity	<i>Halobacillus</i>	P-solubilization, IAA production and biocontrol activity	<i>Salicornia europaea</i>	Zhao et al. (2016)
	<i>Halomonas</i>	IAA production and ACC deaminase activity	<i>Salicornia bigelovii</i>	Rueda-Puente et al. (2010)
	<i>Virgibacillus</i>	P-solubilization and siderophore production	<i>Acacia</i> spp.	Yadav et al. (2015c)
	<i>Micrococcus</i>	P-solubilization and siderophore production	<i>Urochloa mutica</i>	Mukhtar et al. (2016)
	<i>Marinococcus</i>	P-solubilization, IAA production and nitrogen fixation	<i>Salicornia</i> spp.	Mapelli et al. (2013)
	<i>Planococcus</i>	P-solubilization and IAA production	<i>Triticum aestivum</i>	Rajput et al. (2013)
	<i>Pseudomonas</i>	P-solubilization, nitrogen fixation, and siderophore production	<i>Hordeum vulgare</i>	Chang et al. (2014)
	<i>Halobacterium</i>	P-solubilization and nitrogen fixation	<i>Oryza sativa</i>	Wang et al. (2009)
	<i>Haloferax</i>	IAA production and biocontrol activity	<i>Suaeda nudiflora</i>	Saxena et al. (2015a)
	<i>Halococcus</i>	P-solubilization and siderophore production	<i>Sporobolus indicus</i>	Yadav et al. (2015c)
Drought	<i>Frankia</i>	P-solubilization and nitrogen fixation	<i>Aristida plumosa</i>	Bhatnagar and Bhatnagar (2009)
	<i>Azotobacter</i>	P-solubilization, IAA production and nitrogen fixation	<i>Artemesia</i> sp.	Hamdi and Yousef (1979)
	<i>Bacillus</i>	P-solubilization, ACC deaminase activity and IAA production	<i>Cupressus dupreziana</i>	Jorquera et al. (2012)
	<i>Kocuria</i>	P-solubilization, ACC deaminase activity and nitrogen fixation	<i>Zygophyllum dumosum</i>	Steinberger et al. (1995)
	<i>Virgibacillus</i>	P-solubilization, IAA, HCN and siderophore production	<i>Triticum aestivum</i>	Verma et al. (2016)
	<i>Azoarcus</i>	Nitrogen fixation, IAA and siderophore production	<i>Leptochloa fusca</i>	Malik et al. (1997)
	<i>Enterobacter</i>	P-solubilization, nitrogen fixation, IAA, HCN and siderophore production	<i>Phoenix dactylifera</i>	Ferjani et al. (2015)
	<i>Halobacterium</i>	P-solubilization and nitrogen fixation	<i>Oryza sativa</i>	Wang et al. (2009)
	<i>Halococcus</i>	P-solubilization and siderophore production	<i>Sporobolus indicus</i>	Yadav et al. (2015c)
Acidity	<i>Lysinibacillus</i>	P-solubilization, IAA, HCN and siderophore production	<i>Triticum aestivum</i>	Verma et al. (2013)
	<i>Methylobacterium</i>	P-solubilization, ACC deaminase activity, IAA, HCN and siderophore production	<i>Triticum aestivum</i>	Wellner et al. (2011)
	<i>Acidithiobacillus</i>	P-solubilization, IAA, HCN and siderophore production	<i>Pinus rigida</i>	Dang et al. (2017)
	<i>Flavobacterium</i>	P and K solubilization and biocontrol activity	<i>Hordeum vulgare</i>	Verma et al. (2014)
	<i>Pseudomonas</i>	P-solubilization, IAA, HCN and siderophore production	<i>Triticum aestivum</i>	Verma et al. (2013)
	<i>Pyrococcus furiosus</i>	P and K solubilization and biocontrol activity	Thermal marine sediments	Gao et al. (2003)

Table 1 (continued)

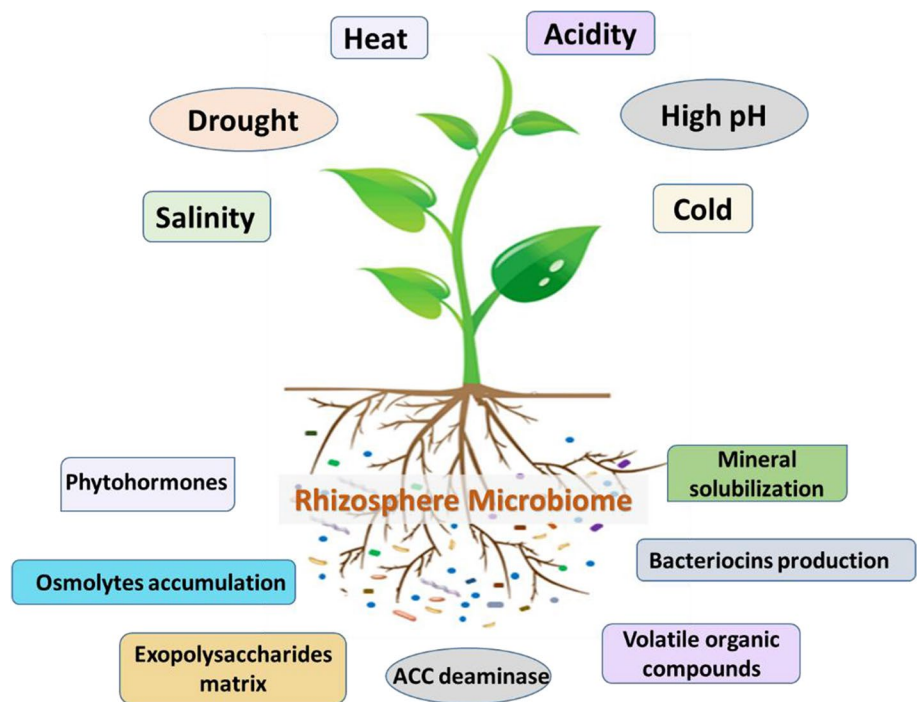
Abiotic stress	Microorganisms	PGP-attributes	Host-plants	References
Alkalinity	<i>Pseudorhodoplanes</i>	IAA production, P-solubilization and nitrogen fixation	<i>Photinia fraseri</i>	Seker et al. (2017)
	<i>Paenibacillus</i>	IAA production, P-solubilization and nitrogen fixation	<i>Photinia fraseri</i>	Seker et al. (2017)
	<i>Curtobacterium</i>	IAA production and P-solubilization	<i>Chrysanthemum morifolium</i>	Zawadzka et al. (2014)
	<i>Sphingomonas</i>	P-solubilization and IAA production	<i>Smallanthus sonchifolius</i>	Moraes et al. (2012)
	<i>Kocuria</i>	P-solubilization, IAA production and nitrogen fixation	<i>Dichanthium annulatum</i>	Mukhtar et al. (2018b)
Heat	<i>Bacillus</i>	P-solubilization, IAA and siderophore production	<i>Triticum aestivum</i>	Verma et al. (2018)
	<i>Arthrobacter</i>	P-solubilization, IAA and biocontrol activity	<i>Triticum aestivum</i>	Kumar et al. (2011)
	<i>Pseudomonas</i>	P-solubilization, IAA, HCN and siderophore production	<i>Triticum aestivum</i>	Vyas et al. (2009)
	<i>Staphylococcus</i>	P-solubilization, HCN and siderophore production	<i>Cupressus dupreziana</i>	Jorquera et al. (2012)
	<i>Streptomyces</i>	P-solubilization and biocontrol activity	<i>Vigna unguiculata</i>	Dimkpa et al. (2008)
	<i>Geobacillus</i>	P-solubilization, IAA and siderophore production and biocontrol activity	Petroleum contaminated Kuwait soil	Zeigler (2014) Al-Hassan et al. (2011)
	<i>Halococcus</i>	P-solubilization and siderophore production	<i>Sporobolus indicus</i>	Yadav et al. (2015c)
Cold	<i>Arthrobacter</i>	P-solubilization, IAA and biocontrol activity	<i>Pinus roxburghii</i>	Singh et al. (2016)
	<i>Bacillus</i>	P-solubilization, IAA and siderophore production	<i>Capsicum annum</i>	Barka et al. (2006)
	<i>Klebsiella</i>	P-solubilization, IAA and siderophore production	<i>Zea mays</i>	Rana et al. (2017)
	<i>Pseudomonas</i>	P-solubilization, nitrogen fixation, IAA, HCN and siderophore production	<i>Solanum tuberosum</i>	Sati et al. (2013)
	<i>Kocuria</i>	P-solubilization, IAA production and nitrogen fixation	<i>Triticum aestivum</i>	Yadav et al. (2015c)
	<i>Methanosarcina</i>	P-solubilization, IAA and siderophore production and biocontrol activity	Siberian permafrost	Morozova and Wagner (2007)
	<i>Methylobacterium</i>	P-solubilization, ACC deaminase activity, IAA, HCN and siderophore production	<i>Triticum aestivum</i>	Saxena et al. (2016)

dupreziana, *Zygophyllum dumosum* and *Leptochloa fusca* (Bhatnagar and Bhatnagar 2009; Buyanovsky et al. 1982). These microorganisms use protein, sugar and some other organic molecules such as ectoine, proline, glycine betaine, trehalose and glutamine to maintain their internal osmotic balance. The rhizosphere microbiome of xerophytes have been studied extensively during the last decade because it is more affected both qualitatively and quantitatively than other desert soil microbiomes (Jorquera et al. 2012).

Gram positive bacteria especially Actinomycetes (*Frankia*, *Kocuria*, *Micrococcus* and *Streptomyces*) may

constitute around 54% of the total microbial diversity in the rhizosphere microbiome of xerophytes (Eppard et al. 1996; Steinberger et al. 1995). Other dominant PGPR genera identified from the rhizosphere of xerophytes included *Bacillus*, *Virgibacillus*, *Azotobacter*, *Pseudomonas*, *Enterobacter* and *Azoarcus* (Ferjani et al. 2015; Malik et al. 1997). *Bacillus licheniformis* strain K11 increased the growth of pepper plant under water stress environments (Table 1; Fig. 1). *Bacillus*, *Pseudomonas* and *Kocuria* are dominant drought tolerant bacterial genera showing various PGP traits (P-solubilizing ability, nitrogen fixation, IAA, HCN

Fig. 1 Overview of microbe-mediated mitigation of abiotic stresses by plants



and siderophore production) and can be used in bioformulations and as biocontrol agents for various crops under rain-fed areas (Jorquera et al. 2012; Kour et al. 2017; Lim and Kem 2013).

Rhizosphere microbiome of plants growing in highly acidic environments

Plant growth is badly affected under acidic conditions due to changes in soil pH and nutrient availability. The sensitive plant tissues maintain their internal pH by exuding ions from root cells by using special enzymes and other proteins (Feliatra et al. 2016; Wellner et al. 2011). Rhizosphere soils are active sites for microbial diversity in acidic environments (Table 1; Fig. 1). A number of acidotolerant PGP bacterial genera including *Lysinibacillus*, *Methylobacterium*, *Acidithiobacillus*, *Flavobacterium* and *Pseudomonas* have been identified and characterized at low pH conditions from various acidic environments (Dang et al. 2017; Feliatra et al. 2016; Wellner et al. 2011).

Rhizosphere microbiomes of grasses such as wheat, rice and maize are considered important for soil health and productivity of these crops under acidic conditions (Verma et al. 2013; Wellner et al. 2011). Microbial siderophores play an important role for their survival under acidic environments and help to alleviate abiotic stresses (Table 1; Fig. 1). These bacteria have siderophore mediated iron uptake system and have ability to change Fe^{3+} to Fe^{2+} under acidic conditions (Sorty et al. 2016; Vansuyt et al. 2007). These PGP

microorganisms are used as biofertilizers to promote plant growth at low pH conditions under acidic environments.

Rhizosphere microbiome of plants growing under alkaline environments

A number of soda lakes have been studied thoroughly for the microbial diversity analysis from naturally occurring alkaline environments. Soda lake water has usually pH ranges 8–10 and even sometimes more than 12 (Antony et al. 2013; Grant and Sorokin 2011). The rhizosphere of plants growing under highly alkaline conditions such as *Photinia fraseri*, *Chrysanthemum morifolium*, *Smallanthus sonchifolius* and *Dichanthium annulatum* represents the distinct microbial diversity because these environments are characterized with ultramafic minerals with more methane and hydrogen and less in carbon content (Seker et al. 2017; Tiago et al. 2004). Microorganisms maintain their cytoplasmic pH by using special enzymes and proteins to balance their functional and structural integrity of cytoplasmic proteins. Mostly alkaliphilic bacteria are able to survive at a broad range of pH (6–10) with optimal pH 7–8 (Jones et al. 1998; Zawadzka et al. 2014). Many alkaliphilic PGP microorganisms such as *Paenibacillus*, *Curtobacterium*, *Sphingomonas*, *Kocuria* and *Arthrobacter* have been reported from a number of alkaline environments (Table 1; Fig. 1). P-solubilizing bacteria identified from highly alkaline environments have ability to produce acids and function properly even at pH 12 and 10% salt concentrations and in this way also contribute to maintain cytoplasmic pH. These bacterial genera have been

studied for their multifarious PGP traits and can be tested for promotion of plant growth and productivity in different crops from alkaline environments (Mukhtar et al. 2018b; Nautiyal et al. 2000).

Rhizosphere microbiome of plants growing under extreme hot environments

High temperature affects plant growth as it decreases germination of seeds and membrane permeability and affects the photosynthesis rate (Xu et al. 2014). Rhizosphere microbiomes of plants growing under hot environments, such as *Sporobolus indicus*, *Triticum aestivum*, *Cupressus dupreziana* and *Vigna unguiculata* have a high potential of plant growth promotion especially for crops growing under hot conditions (Table 1; Fig. 1). PGP bacteria enhance plant growth directly or indirectly by phytohormones production, nitrogen fixation, mineral solubilization (P, Zn and K) and production of siderophores and HCN (Mukhtar et al. 2017; Vyas et al. 2009). Mineral solubilizing bacteria have potential to solubilize P, K, aluminium (Al) and silicon (Si) ions from unavailable to soluble forms by producing organic acids, e.g., acetic acid, formic acid, citric acid, gluconic acid, etc. in hot environments (Verma et al. 2014). Many PGP bacterial genera including *Bacillus*, *Arthrobacter*, *Pseudomonas*, *Staphylococcus* and *Streptomyces* can be used in bioformulations and for crops growing under hot climates (Dimkpa et al. 2008).

Rhizosphere microbiome of plants growing in extreme cold environments

Plants growing under extreme environments such as *Pinus roxburghii*, *Capsicum annum*, *Zea mays*, *Solanum tuberosum* and *Triticum aestivum* survive either through freezing tolerance or through avoiding super cooling of tissue water (Thomashow 2010). Psychrophilic microorganisms have the ability to grow well and show maximum microbial activity at very low temperature as compared to mesophiles (Table 1; Fig. 1). PGP bacteria associated with the cold tolerant plants have ability to induce drought and cold stresses tolerance by production of phytohormones, mineral solubilization, activation of defense-related proteins and enzymes, antioxidants and production of epoxy polysaccharides (Kaushal and Wani 2016; Yadav et al. 2015a). Many cold-adapted PGP microorganisms, e.g., *Arthrobacter*, *Klebsiella*, *Bacillus*, *Kocuria* and *Methylobacterium* were identified and studied from plants growing in different low temperature conditions (Singh et al. 2016; Yadav et al. 2015a, d). Rana et al. (2017) characterized total 66 endophytic bacterial isolates from maize plants from Indian Himalayan regions. These bacterial strains have ability to solubilize P, Zn and K, fix atmospheric nitrogen,

and produce phytohormones, HCN and siderophores. Psychrophilic PGP microorganisms can be used as bioformulations to enhance plant growth for plants growing in cold environments, e.g., hilly regions (Table 1; Fig. 1).

Meta-omics approaches to mitigate abiotic stresses in plants

Meta-omics approaches facilitate the study of microorganisms living at extreme conditions from various environments. With the help of omics technologies, microorganisms can be studied at genomic, transcriptomics and proteomics levels (Yuan et al. 2012). Meta-omics techniques have been used to study plant-associated microbes from a number of extreme environments. These approaches help to understand complex defense signals produced by plants in response of abiotic stresses (Schenk et al. 2012). Meta-omics approaches can be used for better understanding and applications of PGP microbes in various extreme environments (Castro et al. 2013).

Metagenomics

It has been estimated that less than 1% of microorganisms can be cultured. So the vast majority of microbial world has only been accessed by using culture-independent methods or metagenomic approaches (Venter et al. 2004; Zeyaulah et al. 2009). Culture-independent molecular techniques mainly focus on the 16S rRNA gene sequences for identification of microorganisms (Zhou et al. 2015). Microbial diversity of different environments can be investigated without cultivation, solely based on the analysis of 16S rRNA sequence and molecular phylogeny (Broaders et al. 2016; Venter et al. 2004). Next generation sequencing techniques like 454 pyrosequencing (Roche) and illumina (sequencing by synthesis) have been used to study the microbial communities with PGP, biocontrol and antibiotic producing traits from the roots of plants from different extreme environments. Shotgun metagenomic analysis allows direct prediction of taxonomy and molecular functions of PGP microorganisms at the gene level.

ACC deaminase genes (*acdS*) have been reported for salt stress alleviation from a number of studies on the effect of PGP bacteria on potato, wheat, maize and rice plants (Nikolic et al. 2011; Orhan 2016). Genes related to the survival of microorganisms at extreme environments such as compatible solutes, heat shock proteins and pH homeostasis have been characterized by using metagenomics analysis (Liljeqvist et al. 2015; Sessitsch et al. 2012).

Metatranscriptomics

Comparison of transcriptome profiles from different PGP microorganisms through mRNA sequencing analysis and microarray approaches is a useful tool to study plant–microbe interactions (Wang et al. 2016). Many stress-induced responses were controlled by proteins and enzymes such as a sigma factor RpoH1. These proteins ultimately induce the many PGP traits such as phytohormones and ACC deaminase production in rhizobacteria to promote under abiotic stresses (Defez et al. 2016). Some stress induced microbial genes activates miRNAs that ultimately increase the expression of genes involved in the alleviation of abiotic stresses in plants such as *Arabidopsis*, *Medicago*, rice and wheat (Trindade et al. 2010). In rice, miRNA169 was used to alleviate drought and salinity stress and miRNA169c was used in tomato plants to overcome drought stress (Zhao et al. 2009; Zhang et al. 2011). Comparison of different miRNAs have been used to study microbe-mediated aluminum stress in two varieties of rice using RT-PCR approach (Lima et al. 2011).

Metaproteomics

‘Metaproteomics’ is defined as the characterization of whole microbial protein complement from an environmental sample at a specific time (Wilmes and Bond 2006). Metaproteomics analyses have been used to study plant–microbe and microbe–microbe interactions (Kosova et al. 2015). A number of previous studies have discussed on importance of metaproteomics from different environments. Metaproteomics studies on plant microbiome help to understand complex metabolic pathways, detection of multiple functions of microbial genes and proteins. The comparative analysis of plant–microbe interactions under stressed and non-stressed conditions help to identify specific proteins. Protein profile of different plant associated microbes with and without stress can be compared to identify different enzymes and proteins involved in abiotic stress alleviation. Microbial communities associated with different crops such as wheat, barley, rice, *Arabidopsis*, maize oilseed rape and soybean growing under abiotic stresses have been studied using metaproteomic techniques (Liu et al. 2015; Wang et al. 2016). Proteomic analyses based studies can be used to identify protein–protein interactions, different proteins involved in metabolic pathways, enzymes and proteins used as osmolytes to maintain intracellular osmotic balance under abiotic stress and proteins associated with cell wall and the cytoskeleton (Kosova et al. 2015).

Conclusions and future perspective

Plants growing under extreme environments have evolved different mechanisms to survive under such harsh conditions. Microbes-mediated stress alleviations have been studied on the basis of environmental adaptations and genetic traits. By using meta-omics approaches, plant beneficial bacteria can be used in a better way for improvement of crop production under abiotic stresses. Studies on plant–microbe interactions using metagenomics, metatranscriptomics, and metaproteomics techniques could produce a multi-layered information on microbes-mediated stress response of plants. PGP microorganisms identified and characterized from the roots of plants growing under extreme environments may be used as bioinoculants and bio-control agents for the better growth of various crops in future. The PGPR induced abiotic stress tolerance in different plants may be involved for production of different extracellular enzymes and other organic compounds to improve soil properties, enhance plant growth and provide as signaling molecules to the plants. More research is needed to find out new roles of microorganisms in plants’ growth 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 future.

Acknowledgements We are highly thankful to Higher Education Commission [Project # HEC (FD/2012/1843)] for research grants.

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