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Biodiversity and biotechnological applications of halophilic microbes for sustainable agriculture

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ABSTRACT

Extreme saline environments represent unique ecosystems for novel microbial biodiversity. The salt-tolerant microbiomes have been reported from diverse saline habitat. The biodiversity of salt-tolerant microbes showed the presence of different groups of microbes including Actinobacteria, Bacteroidetes, Euryarchaeota, Firmicutes, Proteobacteria, and Spirochaetes. The salt-tolerant plant growth promoting (PGP) microbes such as *Ammoniphilus, Arthrobacter, Azospirillum, Bacillus, Brevibacillus, Brevibacterium, Haloarcula, Halobacillus, Halococcus, Haloferax, Halolamina, Halomonas, Halorubrum, Haloterrigena, Lysinibacillus, Marinobacter, Marinospirillum, Oceanobacillus, Paenibacillus, Penicillium, Pontibacillus, Pseudomonas, Sediminibacillus, Sporosarcina, Streptomyces, Thalassobacillus*, and *Thermonema* have been isolated and characterized for plant growth under the salinity stress. The halophilic microbes have ability to produce phytohormones (indole acetic acids, gibberellic acids, and cytokinin), solubilize and bind nutrients (phosphorus, potassium, zinc, and siderophores), besides eliciting plant defense reactions against pathogens, also help in plant growth under harsh saline environments. The halophilic PGP microbes increase the plant growth, yields, and nutrient uptake under the saline condition. In the present review, the biodiversity of halophilic microbes from diverse ecosystems, its functional PGP attributes and mechanisms of action for amelioration of salt stress, plant growth, and soil health for sustainable agriculture have been discussed. The salt-tolerant microbes with multifarious PGP attributes could be applied for plant growth and ameliorations of salt stress.

1. INTRODUCTION

Soil salinity is one of the major limiting factors for plant growth and its productivity worldwide. The research on salt tolerance microbiomes have been increased to improve crop growth and yield for sustainable agriculture. Salinity is a natural feature of ecosystems in arid and semiarid regions and can also be induced by anthropogenic activities. Nearly 20% of the world's cultivated lands are affected by salinity, which is responsible for significant crop production losses. The hypersaline environment is one of the most extreme habitats with respect to the sodium chloride concentration. The salt concentrations in hypersaline habitats range from >15% to saturation, with pH values from acidic to alkaline (pH 6-11). The microbiomes of various saline environments are salt-loving microbes, with the capacity to tolerate abiotic stress of salinity (2.57-5.48M NaCl). Halotolerant microbes specifically require salt for growth and development under the normal and saline conditions. The salt-loving microbes can be grouped as true halophiles (15-30% NaCl), moderate halophiles (3-15% M NaCl), and slight halophiles (1-2% NaCl) [1].

Halophilic/halotolerant microbes have been isolated from diverse hypersaline environments such as solar salterns, hypersaline lakes, the Dead Sea, hypersaline microbial mats, and underground salt deposits. The salt-tolerant plant microbiomes (epiphytic, endophytic, and rhizospheric) have been sort out and characterized for tolerance to abiotic stress of salinity and other beneficial attributes worldwide [2]. The salt-tolerant microbes have been discovered from different phyla including Actinobacteria, Bacteroidetes, Euryarchaeota, Firmicutes, Proteobacteria, and Spirochaetes. Halophilic microbes such as *Ammoniphilus, Arthrobacter, Azospirillum, Bacillus, Brevibacillus, Brevibacterium, Haloarcula, Halobacillus, Halococcus, Haloferax, Halolamina, Halomonas, Halorubrum, Haloterrigena, Lysinibacillus, Marinobacter, Marinospirillum, Oceanobacillus, Paenibacillus, Penicillium, Pontibacillus, Pseudomonas, Sediminibacillus, Sporosarcina, Streptomyces, Thalassobacillus*, and *Thermonema* have been isolated and characterized for plant growth promotion. The plant growth promoting (PGP) attributes included biological nitrogen fixation; 1-aminocyclopropane-1-carboxylate (ACC) deaminase activity; solubilization zinc, potassium and phosphorus; production of ammonia, hydrogen cyanide, siderophores (Fe-chelating compounds), phytohormones (cytokinin, gibberellic acids, and indole acetic acids); and other secondary metabolites. In the present review, the biodiversity of halophilic microbes from diverse ecosystems, its functional PGP attributes and mechanisms of action for amelioration of salt stress,

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plant growth, and soil health for sustainable agriculture have been discussed.

2. BIODIVERSITY OF HALOPHILIC MICROBES

Microbial research in saline environments (solar salterns, hypersaline lakes, the Dead Sea) has fascinated the curiosity of scientists due to biotechnological application of salt-tolerant microbes in agriculture, industry, and medicine. The salt-tolerant microbes could be applied as biofertilizers under saline condition for growth, yield, and soil health for sustainable agriculture. The novel and efficient enzymes producing halophilic microbes may be used in different industrial processes. There are many novel species of halophilic microbes including *Actinopolyspora mortivallis* [3], *Halothermothrix orenii* [4], *Natrinema versiforme* [5], *Halomonas marisflavae* [6], *Bacillus marisflavi* [7], *Arcobacter halophilus* [8], *Nesterenkonia aethiopica* [9], *Aquisalimonas asiatica* [10], *Amycolatopsis halophila* [11], *Pontibacillus yanchengensis* [12], *Streptomyces chilikensis* [13], *Prauserella isguenensis* [14], *Marinirhabdus gelatinilytica* [15], and *Haloprofundus marisrubri* [16], which have been sorted out from crops growing under saline conditions, saline lakes, and hypersaline soils worldwide.

The hypersaline region represents hot spots of biodiversity of several novel and efficient salt-tolerant microbial (archaeal bacterial and fungal) species which have been reported from different hypersaline. Archaea is one of the most abundance microbes reported from extreme saline and hot springs environments. There are very few reports of archaea as associated with plants such as maize, rice, and halophytic plant (*Abutilon, Cressa, Sporobolus,* and *Suaeda nudiflora*) [17-19]. Archaea have been reported as unculturable from maize [20] and rice crop [21], whereas culturable archaea have been reported from *Abutilon, Cressa, Sporobolus, S. nudiflora* [22]. The most dominant microbes belong to domain Eubacteria which included different genera such as *Alkalibacillus, Amphibacillus, Amycolatopsis, Arthrobacter, Bacillus, Brevibacterium, Corynebacterium, Exiguobacterium, Haloactinomyces, Halobacillus, Haloglycomyces, Halomonas, Lysinibacillus, Microbacterium, Micrococcus, Oceanobacillus, Oceanobacillus, Paenibacillus, Paraliobacillus, Planococcus, Pontibacillus, Pseudomonas, Rhodococcus, Salinibacillus, Sediminibacillus, Sporosarcina, Staphylococcus, Streptomonospora, Streptomyces, Tenuibacillus, Thalassobacillus,* and *Virgibacills* have been reported from diverse saline environments. Along with bacterial isolates, the halophilic fungi such as *Alternaria, Aspergillus, Cladosporium, Debaryomyces, Hortaea, Myrothecium, Penicillium, Piriformospora, Saccharomyces, Stemphylium, Sterigmatomyces, Trichoderma, Ulocladium,* and *Wallemia* have been reported from the diverse hypersaline environment and hypersaline lakes worldwide [17,23,24]. Microbiome of saline environments, especially halophilic fungi, has become one of the richest bioresources for industrially important molecules and enzymes. Among different groups of fungi, the isolated from deep sea are most important in pharmaceutical industry, due to the production of secondary metabolites under the harsh saline conditions. The hypersaline habitats are only beginning to be investigated for bioactive natural products.

Halophilic microbes have been reported from different phylum including Actinobacteria, Bacteroidetes, Euryarchaeota, Firmicutes, Proteobacteria, and Spirochaetes (Fig. 1). Among different groups of bacteria, Actinobacteria are most dominant and are ubiquitous in nature and have been isolated from diverse extreme environments (extreme temperatures, pH, salinities, pressure, and drought) and associated with plant growing in different habitat. The rhizospheric actinobacteria have been reported, biochemically characterized, and identified using 16S rRNA gene sequencing. Based on a comprehensive literature analysis, members of phylum actinobacteria have been reported from different genera such as *Acidimicrobium, Actinomyces, Arthrobacter, Bifidobacterium, Cellulomonas, Clavibacter, Corynebacterium, Frankia, Microbacterium, Micrococcus, Mycobacterium, Nocardia, Propionibacterium, Pseudonocardia, Rhodococcus, Sanguibacter,* and *Streptomyces* from saline habitat [25,26].

The members of Firmicutes are widely dispersed in nature, easy to multiply, have a long shelf life when sporulated, and are nonpathogenic. Among *Bacillus* and *Bacillus*-derived genera, *Bacillus thuringiensis, Bacillus subtilis, Bacillus pumilus, Bacillus mycoides, Bacillus megaterium,* and *Bacillus firmus* are ubiquitous in rhizosphere saline soil [1,27,28]. The genus *Bacillus* consists of a heterogenic group of endospores forming Gram-positive rods, which survive for extended periods under adverse environmental conditions due to endospores. The phylum proteobacteria are Gram-negative bacteria which included α/β/γ/δ-proteobacteria, which has been reported from different saline environments. Among proteobacteria, α-proteobacteria grows at very low levels of nutrients and includes agriculturally imperative bacteria capable of inducing *Azospirillum,* N_2-fixation in symbiosis with plants. The β-proteobacteria is highly metabolically diverse and contains chemolithoautotrophs, heterotrophs, and photoautotrophs, whereas the γ-proteobacteria is the largest class in terms of species *Pseudomonas* and *Azotobacter* [17,29].

3. HALOPHILIC MICROBES FOR SUSTAINABLE AGRICULTURE

Soil salinity is a major problem facing the agricultural production in many fields and soil infertility in the treatment or the regions due to the presence of high concentrations of salt. The excess of soluble salt is present in saline soil and Na^+ with negative-charged clay particles present in hypersaline soil. The growth of plant/crops has been inhibited due to the presence of high concentration of sodium salt in the saline soil which occurs through natural or human-induced processes. The natural salinity results from the accumulation of salts over a long period of time due to weathering process. Accumulation of salt such as sodium chloride, calcium chloride, and magnesium chloride have been done continuous by weathering process (breaks down rock and releases soluble salts). The plant microbiomes have been selected by plants itself by producing different nutrients into nearby environments. The beneficial and efficient microbes have attached to roots by different plant, due to their root exudates. The epiphytic microbes have attached to phyllosphere part of plant due to secretion of diverse sticky substances by plants. Thus, the plant-microbes interaction has been developed, and microbial community utilized the constituents of exudates as sources of energy [2,30]. The microbiomes isolated from crops growing in saline ecosystems are able to promote the plant growth. The plant microbiomes have been reported as epiphytic, endophytic, and rhizospheric and have been characterized for plant growth promotion under *in vitro* and *in vivo* condition of salinities stress. The PGP microbes belonged to different genera such as *Achromobacter, Azotobacter, Bacillus, Burkholderia, Methylobacterium, Micrococcus, Micromonospora, Pantoea, Pseudomonas,* and *Streptomyces* as epiphytic microbes; Achromobacter, *Bacillus, Burkholderia, Microbiospora, Micromonospora, Nocardioides, Pantoea, Planomonospora, Pseudomonas, Streptomyces,* and *Thermomonospora* as endophytic microbes; and *Azospirillum, Alcaligenes, Arthrobacter, Acinetobacter,*

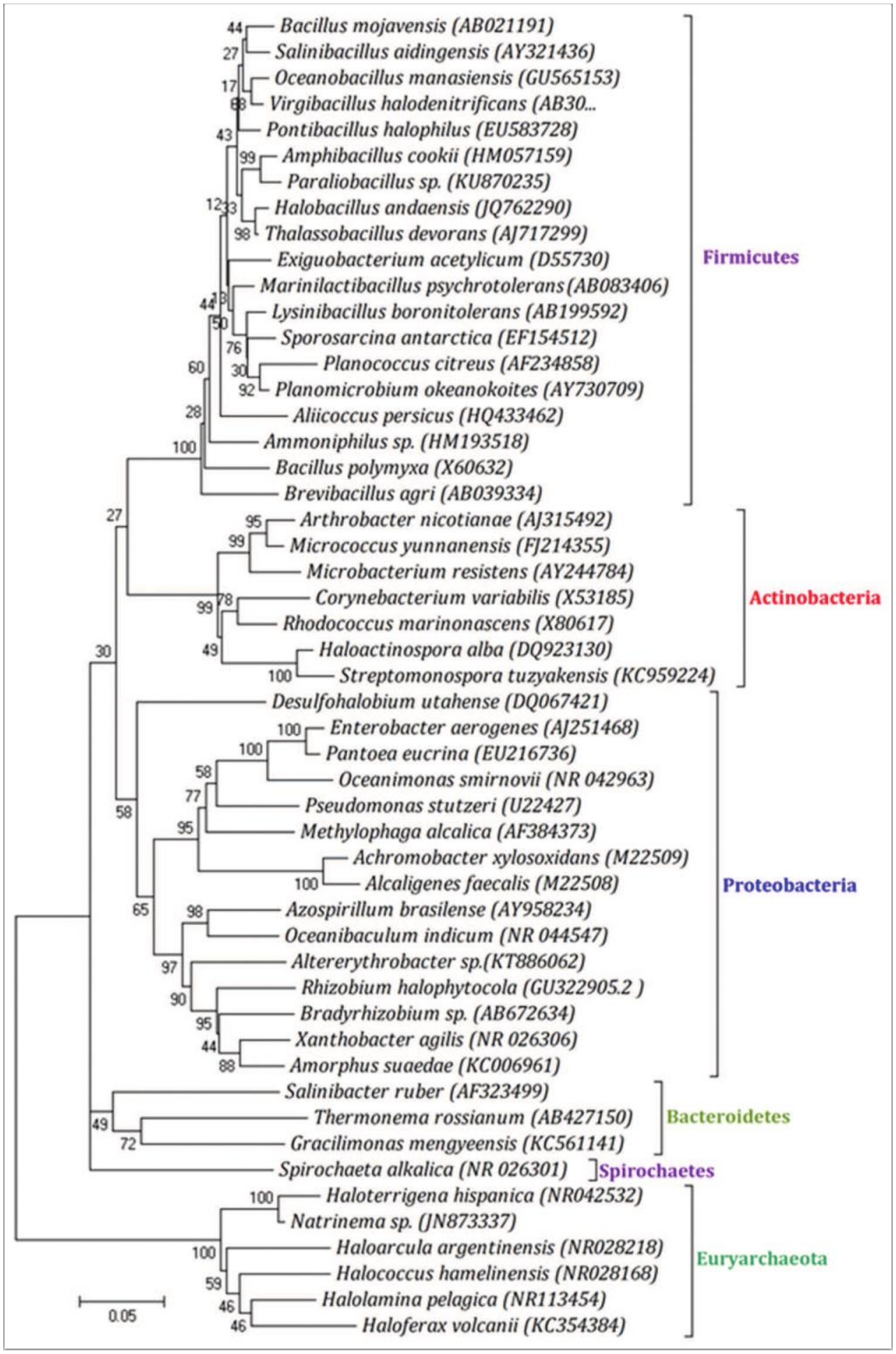

Fig. 1: Phylogenetic tree showed the relationship among halophilic microbes. 16S rRNA gene sequences obtained from NCBI database. The sequence alignment was performed using the CLUSTAL W program, and trees were constructed using maximum likelihood method with algorithm using MEGA4 software. One thousand bootstrap replicates were performed. Bootstrap values are indicated on the branches.

Bacillus, *Paenibacillus*, *Burkholderia*, *Enterobacter*, *Erwinia*, *Flavobacterium*, *Methylobacterium*, *Pseudomonas*, *Rhizobium*, and *Serratia as* rhizospheric microbes from crops growing in diverse agro-ecosystems [18,26,31,32].

The plant microbiomes can promote plant growth directly by the production of phytohormones (indole acetic acids, gibberellic acids, and cytokinin), solubilization and bindings of nutrients (phosphorus, potassium, zinc, and siderophores), biological nitrogen fixation, and ACC deaminase activity. In another plant growth, mechanisms of in-direct by the production of ammonia, hydrogen cyanide, siderophore (Fe-chelating compounds), and other secondary metabolites which elicits plant defense against different plant pathogens also help in plant growth under harsh saline environments [26,32,33] (Table 1). The

Table 1: Role of halophilic microbes in plant growth promotion under the saline environments.

Microbes	Strain	Response	Reference
Aeromonas hydrophila	MAS-765	Alleviate salinity, growth	[51]
Bacillus insolitus	MAS17	Alleviate salinity, growth	[51]
Bacillus sp.	MAS617	Alleviate salinity, growth	[51]
Staphylococcus kloosii	EY37	Alleviate the moderately salt	[52]
Kocuria erythromyxa	EY43	Alleviate the moderately salt	[52]
Pseudomonas aurantiaca	TSAU22	Growth and salinity tolerate	[53]
Pseudomonas chlororaphis	TSAU13	Growth and salinity tolerate	[53]
Pseudomonas extremorientalis	TSAU20	Growth and salinity tolerate	[53]
Pseudomonas extremorientalis	TSAU6	Growth and salinity tolerate	[53]
Pseudomonas fluorescens	153	Salinity stress, growth	[54]
Pseudomonas putida	108	Salinity stress, growth	[54]
Pseudomonas putida	TSAU1	Growth and salinity tolerate	[53]
Arthrobacter sp.	AS 18	Growth and salt stress	[55]
Bacillus licheniformis	RS656	Ameliorates salt stress, nutrient uptakes	[56]
Brevibacterium iodinum	RS16	Ameliorates salt stress, nutrient uptakes	[56]
Nitrinicola lacisaponensis	SL 11	Growth salt stress	[55]
Zhihengliuela alba	RS111	Ameliorates salt stress, nutrient uptakes	[56]
Metarhizium anisopliae	LHL07	Growth and salt stress	[57]
Azotobacter chroococcum	C5	Alleviated the saline stress	[58]
Aeromonas vaga	BAM-77	Growth and yield	[59]
Bacillus amyloliquefaciens	SN13	Salt tolerance in rice	[60]
Pseudomonas fluorescens	YsS6	Plant growth	[61]
Pseudomonas migulae	8R6	Plant growth	[61]
Paenibacillus xylanexedens	PD-R6	Root growth and nutrient uptake	[62]
Enterobacter cloacae	PD-P6	Root growth and nutrient uptake	[62]
Achromobacter xylosoxidans	249	Growth and SOD activity	[63]
Bacillus amyloliquefaciens	BNE12	Growth and alleviate salinity	[26]
Bacillus licheniformis	HSW-16	Growth and productivity	[64]
Bacillus methylotrophicus	BNE2	Growth and alleviate salinity	[26]
Enterobacter sp.	12	Growth and SOD activity	[63]
Paenibacillus xylanexedens	BNE18	Growth and alleviate salinity	[26]
Planomicrobium okeanokoites	BNE8	Growth and alleviate salinity	[26]
Pseudomonas sp.	33	Growth and SOD activity	[63]
Serratia marcescens	73	Growth and SOD activity	[63]
Trichoderma longibrachiatum	T6	Seedling, salt stress	[65]
Bacillus aquimaris	DY-3	Alleviated the salt stress	[66]
Chryseobacterium gleum	SUK	Root and shoot length, nutrient uptakes	[67]
Enterobacter cloacae	ZNP-3	Resistance against salt	[68]
Klebsiella sp.	SBP-8	Plant growth and yield	[69]
Mesorhizobium sp.	MBD26	Nodulation and plant biomass	[70]
Pseudomonas sp.	ISE-12	Growth promotion	[71]
Sphingomonas sp.	LK11	Alleviates salinity stress	[72]
Xanthomonadales sp.	CSE-34	Growth promotion	[71]

SOD: Superoxide dismutase

halophilic/halotolerant may promote plant growth in terms of increased seedling germination rates, roots and shoot length, biomass, nitrogen, phosphorus and potassium (NPK) content, chlorophyll content, protein content, yield, and tolerance to salinity stress. The microbiomes, the multifunctional PGP attributes, could be used as biofertilizers or bio-inoculants which will be finally fit into long-term for high yield and soil fertility for sustainable agriculture. The soil salinity is one of the major limiting factors to plant growth and its productivity. Along with

PGP microbes for growth and ameliorations of salinity stress, many other technologies have been implicated in the improvement of salt tolerance in crops. Sustainable agriculture requires the use of strategies to increase or maintain the current rate of food production. The PGP microbes as biofertilizers may alternative to conventional agricultural technologies.

The chemical fertilizers may be reduced by the use of microbes with multifunctional PGP attributes. The chemical fertilizers NPK are necessary for plant growth and high-yield productivity. The applications of these chemicals may be reduced/replaced by nitrogen-fixing, P-solubilizing, and K-solubilizing/mobilizing microbes (NPK) as biofertilizers an eco-friendly technologies without harming the environment for sustainable agriculture. The nitrogen-fixing microbes (symbiotic, non-symbiotic, and free-living) such as *Anabaena, Nostoc, Azospirillum, Azospirillium, Azotobacter, Beijerinckia, Clostridium, Drexia, Enterobacter, Gluconacetobacter, Klebsiella, Pseudomonas,* and *Rhizobium* have been reported and characterized for biological nitrogen fixation under the saline conditions [34-36]. Among different micronutrients, phosphorus and potassium are essential for plant growth and development under the natural and harsh environmental conditions [29,37,38]. P-solubilization is a common attributes among different groups of microbes including haloarchaea (*Haloarcula argentinensis, Haloferax alexandrinus, Haloferax larsenii, Haloferax volcanii, Halolamina pelagica, Halostagnicola kamekurae, Haloterrigena thermotolerans,* and *Natronoarchaeum mannanilyticum*); halophilic bacteria (*Azotobacter, Burkholderia, Citrobacter, Enterobacter, Pantoea,* and *Pseudomonas*); and salt-tolerant fungi (*Aspergillus, Penicillium, Trichoderma,* and *Piriformospora*) which have been isolated and characterized for P-solubilization [22,39-43]. K-solubilizing microbes such as *Achromobacter, Arthrobacter, Bacillus, Duganella, Ensifer, Enterobacter, Exiguobacterium, Klebsiella, Lysinibacillus, Methylobacterium, Microbacterium, Ochrobactrum, Paenibacillus, Penicillium, Planococcus, Pseudomonas, Psychrobacter, Rhodobacter, Salmonella, Sphingobacterium,* and *Stenotrophomonas* have been isolated and characterized for K-solubilization under *in vitro* and *in vivo* conditions [24,26,28,35,44].

The plant microbiomes produced different types of plant growth-regulating hormones such as cytokinins and gibberellic acids and indole acetic acids. Indole acetic acids production is most common among all growth-regulating substances, and it has been produced by all types of plant-microbes interaction, for example, epiphytic, endophytic, and rhizospheric microbes. The gibberellic acids are most typical plant growth-regulating hormones, which have been produced by rhizospheric microbes, whereas cytokinins production has been reported by epiphytic/phyllospheric microbes. The production of such growth regulators by different groups of microbes provides numerous profits to the plants including the root growth, water absorption, and uptake of micronutrient from soil to plant and also ameliorates different abiotic stresses such as cold, heat, drought, and salinity. The plant microbiomes such as *Arthrobacter, Azospirillum, Bacillus, Bradyrhizobium, Burkholderia, Enterobacter, Exiguobacterium, Lysinibacillus, Methylobacterium, Microbacterium, Ochrobactrum, Paenibacillus, Pantoea, Penicillium, Planococcus, Pseudomonas, Psychrobacter, Rhizobium, Rhodobacter, Salmonella, Sphingobacterium,* and *Stenotrophomonas* have been reported to produced different PGP phytohormones [36,45,46].

The other PGP attributes for amelioration of salt stress are ACC deaminase activities by halophilic microbes. The microbes with ACC deaminase activities have the ability to decrease plant ethylene levels under the abiotic stress of salinity. Plant microbiomes such as *Arthrobacter, Bacillus, Burkholderia, Enterobacter, Methylobacterium, Paenibacillus, Pantoea, Penicillium, Pseudomonas, Rhizobium, Rhodobacter,* and *Serratia* have been reported as having the ability to decrease plant ethylene levels under the abiotic stress [35,44,45,47]. Along with direct PGP attributes, the plant microbiomes also possess some indirect PGP attributes such as the production of ammonia, hydrogen cyanide, siderophore (Fe-chelating compounds), antibiotics, antimicrobial substances, pigments, and some hydrolytic enzymes (β-1, 3-glucanase, chitinases, pectinase and cellulase) [26,48,49]. These attributes help to protect crops from different plant pathogens and using these microbes as biocontrol in form of biofertilizers may increase crops productivity [50]. The most promising microbes which promote the plant through in-direct PGP mechanisms belong to different genera such as *Aeromonas, Bacillus, Chryseobacterium, Enterobacter, Metarhizium, Nitrinicola, Planomicrobium, Pseudomonas, Sphingomonas, Trichoderma, Xanthomonadales,* and *Zhihengliuela* [34,41,45].

Biofertilizers are basically the microbes which basically bring about the enrichment of the nutrients of the soil by enhancement of the availability of the micronutrients to different cereal crops. The plant nutrients are one of the most essential components for sustainable agriculture. The production of the healthy crops so as to meet the demands of the world's expanding population mainly relies on the type of the fertilizers which are basically used to supplement all the nutrients to the plants, but more reliability on the chemical fertilizers is damaging the environmental ecology as well as affecting the human health with great severity. Thus, the use of the microbes as biofertilizers is considered as an alternative to chemical fertilizers so as to improve the fertility of the soil as well as increasing the productivity of the crops in sustainable farming. The plant microbiomes are considered to be the efficient and a novel tool for providing extensive benefits to the agriculture. The rhizospheric microbes basically colonize the roots and stimulate the growth under the natural as well as saline conditions. Halophilic microbes are contributing to the growth and sustenance of plants through various PGP activities under saline environments. These halophilic microbes help the plant in amelioration of salt stress and also promote the growth of plant and increase the soil fertility. There are many such reports on halophilic microbes including archaea, bacteria, and fungi used for ameliorations of salt stress and plant growth promotion for sustainable agriculture.

4. CONCLUSION AND FUTURE PROSPECT

Extreme environment is the major limiting factors to plant growth and its productivity. The research on salt tolerance microbiomes has been increased to improve crop growth and yield for sustainable agriculture. Potentially, PGP microbes can enhance plant resistance toward biotic and abiotic stresses as well as ameliorates the salt stress in crops. The microbes, the multiple PGP attributes, could be used as biofertilizers for high output yield to maintain the fertility of soil for sustainable agriculture. These potential PGP microbes will be eco-friendly from environments and human health. Hence, the research has to be focused on the discovery of novel and efficient microbial biodiversity from unexplored area such as hypersaline and drought region, which can be utilized for plant growth promotion and soil health. To replace the chemical NPK fertilizers, nitrogen-fixing, P-solubilizing, and K-solubilizing (NPK) microbiomes should be utilized as biofertilizers in large-scale crop production. In the future, the research on PGP mechanisms and its application for ameliorations of salt stress as well as in other biotechnological application such as microbe-mediated bioremediations and production of industrially and pharmaceutically important molecule from microbes harbor in diverse extreme environments will be increased. The beneficial microbes may be also screened for different probiotic attributes, which may be used for human health and nutrition. The research on microbiomes from extreme environments and plant microbiomes is very promising and will have noteworthy economic and environmental impacts in the future.

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