

Microbiome of Halophytes: Diversity and Importance for Plant Health and Productivity

Salma Mukhtar, Kauser Abdulla Malik*, and Samina Mehnaz

Department of Biological Sciences, Forman Christian College (A Chartered University), Ferozepur Road, Lahore 54600, Pakistan

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The distribution of saline soils on more than half a billion hectare worldwide warrants attention for their efficient, economical and environmentally acceptable management practices. Halophytes are progressively utilized for human benefits. Halophytes microbiome contributes significantly to plant performance and can provide information regarding complex ecological processes involved in osmoregulation of halophytes. Microbial communities associated with the rhizosphere, phyllosphere and endosphere of halophytes play an important role in plant health and productivity. Members of plant microbiome belonging to domains Archaea, Bacteria and kingdom Fungi are known to be involved in osmoregulation of halophytes. Mostly halophilic microorganisms use compatible solutes such as glycine betaine, proline, trehalose, ectoine and glutamic acid to survive under salinity stress conditions. Plant growth promoting rhizobacteria (PGPR) enhance plant growth and help to elucidate the salinity tolerance. The detailed studies on metabolic pathways of plants have shown that PGPRs contribute to plant tolerance by affecting the signaling network of plants. Phytohormones (indole-3-acetic acid and cytokinin), 1-aminocyclopropane-1-carboxylic acid deaminase (ACC) biosynthesis, exopolysaccharides, halocins and volatile organic compounds function as signaling molecules for plants to elicit salinity stress. This review has mainly focused on the functions of plant microbiome and how these microorganisms impact on halophyte health and growth.

Keywords: Halophyte microbiome, PGPR, phytohormones, ACC deaminase, exopolysaccharides

Introduction

Soil salinity is one of the major abiotic stresses that affect agriculture areas worldwide. The salt affected area constitutes more than 6% of the world's total land area and this has occurred over a period of time in arid and semi-arid zones [1, 2]. Soluble ions in soils affect plant growth by reducing photosynthesis and transpiration from plant roots. Soil salinity also cause a direct effect on the availability of nutrients and metabolic process in the plant tissues or indirect effect of salt altering the structure, permeability and aeration of soil [3–5]. In order to overcome this situation a biological approach

has been proposed to economically utilize these saline wastelands. One of the important components of this approach is the rhizosphere of the plants naturally growing in such environments. There are multiple biochemical pathways that facilitate the ability of plants to tolerate stress due to salt and maintaining homeostasis of ions [6, 7]. Halophytes such as *Suaeda fruticosa*, *Kochia indica*, *Atriplex amnicola* and *Salsola stocksii* may contribute significantly to the developing world's supply of food, fiber, fuel and fodder [8, 9]. For areas where farm land has been salinized by poor irrigation practices or that overlies reservoirs of brackish water or for coastal desert regions, these plants could be successfully grown [1, 10, 11].

Microbial diversity of extreme environments such as arid regions, saline, thermophilic and acidic is especially important because microorganisms present in these

*Corresponding author

Tel: +92-42-99231581

E-mail: kausermalik@fccollege.edu.pk

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habitats have special genetic and physiological characteristics to survive and grow in these extreme conditions [12–14]. The physiology and metabolism of the halophytes are affected by plant microbiome which include plant growth promoting rhizobacteria (PGPR), ectomycorrhizal fungi (AMF) and pathogenic microorganisms [15, 16]. The rhizosphere of halophytes harbors a variety of microorganisms (microbiome) that have ability to promote plant growth by increasing the availability and uptake of carbon, nitrogen and minerals from soil [17–19]. Some species of PGPRs such as *Rhizobium*, *Klebsiella*, *Pseudomonas* and *Enterobacter* are facultative endophytes and live in intercellular spaces of host tissues to establish a mutual beneficial association [20–22]. The phyllosphere is a more dynamic environment than the rhizosphere of plants, so, the microbial communities associated with leaves are not uniform and is influenced by number of stomata, leaf veins and hairs [23, 24]. Studies on the microbial diversity associated with the phyllosphere of *Salsola* have shown that Actinobacteria and Proteobacteria are the most abundant phyla [25, 26].

Since most of previous studies on halophytes have focused on physiological and genetic regulation of salinity resistance, nevertheless, salinity tolerance in halophytes is also connected with complex microbial ecological processes within their rhizosphere and phyllosphere. Because plant microbe interactions in saline habitats have been sparsely studied, we mainly focus on halophyte microbiomes diversity and functions. First, we will discuss about different strategies that halophilic microorganisms adapt to survive under hypersaline environments. Second, we will give an overview of role of halophyte microbiomes in salinity tolerance. Finally, we will discuss about beneficial as well as pathogenic microorganisms that colonize in the rhizosphere, phyllosphere and endosphere of halophytes.

Halophyte rhizosphere and root endosphere microbiome

The rhizosphere is the soil region around plant roots which influences the root growth by production of different root exudates. There are a variety of compounds

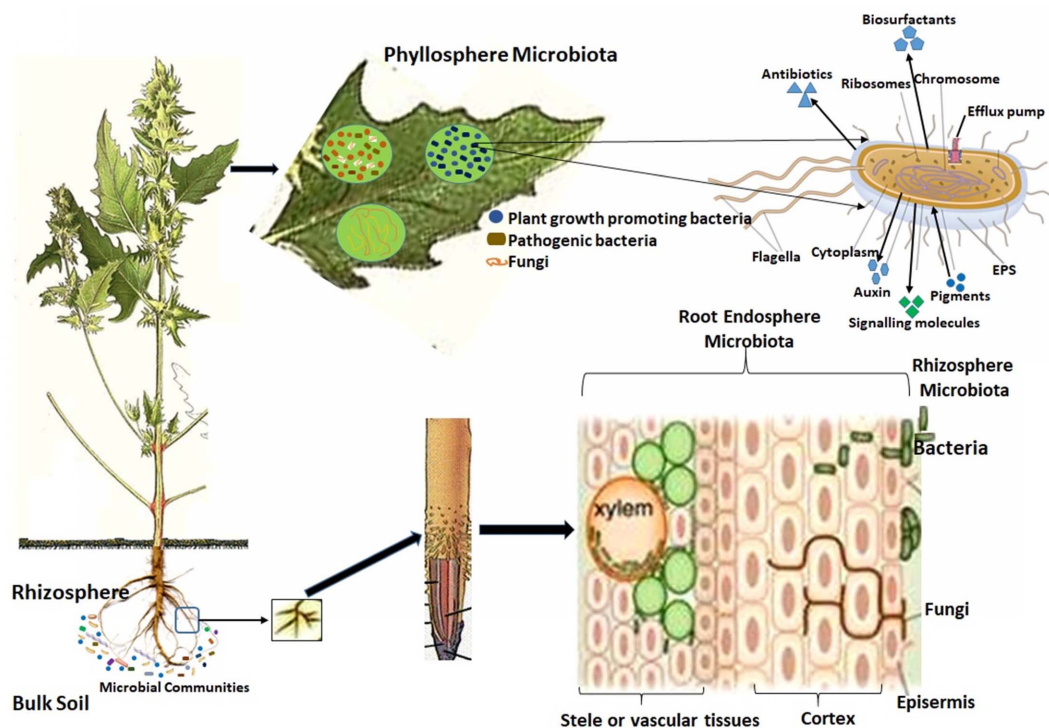


Fig. 1. Overview of a halophyte microbiome. Functions and impact of microbial communities in the rhizosphere, endosphere and phyllosphere of halophyte.

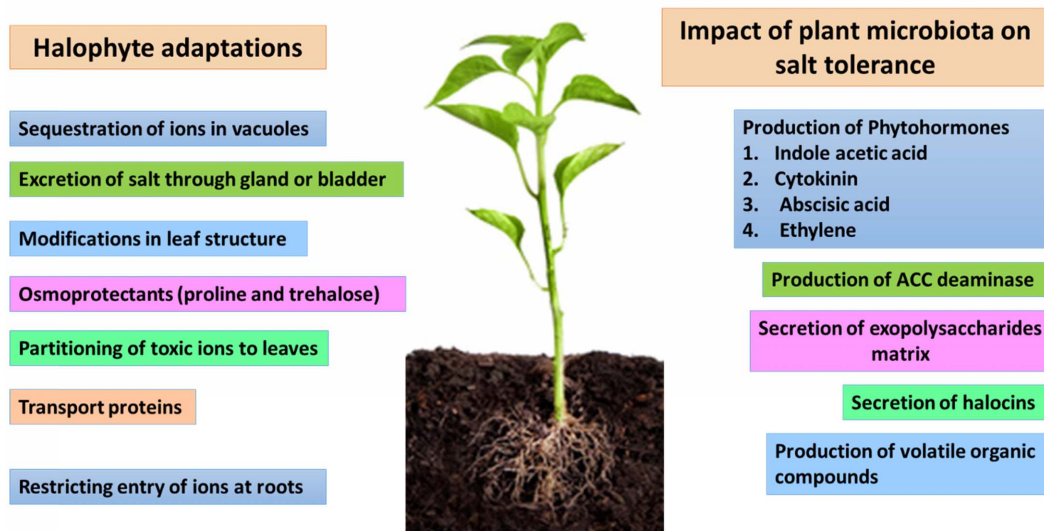


Fig. 2. Comparison of salinity tolerance by halophyte microbiome and plant. Halotolerant and halophilic PGPRs strains by production of phytohormones, ACC deaminase, exopolysaccharides, halocins and volatile organic compounds.

(sugars, amino acids, vitamins, growth factors and hormones) produced by plant roots [27, 28]. Rhizosphere is the site of immense microbial activity. Rhizosphere microbiome structure and composition mainly depends on the roots exudates of plants [29, 30]. Composition of rhizosphere microbiome may vary among different plant species and it affects changes in plant development and growth [31]. Microbial communities may be different in the rhizosphere of the same plant at various development stages (Fig. 1). Plant growth promoting rhizobacteria (PGPR) may provide the plant with different accessible nutrients such as nitrogen (N) and phosphorus (P) [32], phytohormones (auxins, cytokinins, gibberellins, ethylene and abscisic acids) that promote plant growth under salt stress conditions [26, 33, 34].

Some PGPR bacteria and archaea have ability to change atmospheric nitrogen to nitrate which is easily available to plants (Fig. 2). It is the major mechanism used by microorganism to enhance plant growth [35]. The best known nitrogen fixing bacteria include *Mesorhizobium*, *Bradyrhizobium*, *Pseudomonas*, *Halobacillus*, *Bacillus*, *Serratia* and *Salinibacter* [36–38]. Many root endophytes can be used as biocontrol agents due to their production of different antibiotic and antifungal compounds [39]. Halotolerant and halophilic *Bacillus* spp, produce hydrolytic enzymes and have been reported as growth inhibitors for fungal pathogens and

they provide protection for different plant diseases [26, 40]. These microorganisms also produce a variety of hydrolytic enzymes and play an important role in suppressing the fungal pathogens such as *Alternaria* sp. and *Fusarium* sp. (Table 1). PGPRs also help plants to survive under harsh conditions like salinity, drought and heat [19, 41].

Halophyte phyllosphere and leaf endosphere microbiome

Microbial communities that colonize at the surface and inside the tissues of aerial parts of plants are collectively known as the phyllosphere. Microorganisms like bacteria, archaea, fungi, yeasts and protists reside in the phyllosphere under nutrient and water deficient environment [42, 43]. Phyllosphere microbiome plays an important role in plant protection against different fungal and bacterial pathogens [44]. Microbial communities in the phyllosphere showed less diversity as compared to the rhizosphere microbial communities (Fig. 1). Culture-independent approaches have revealed that phyllosphere microbiome has a major role in the bioremediation of polluted gases which are present in the atmosphere [45, 46].

Bacterial strains isolated from the phyllosphere produce different hydrolytic enzymes and biocontrol agents

Table 1. Halophilic bacteria and archaea isolated from different hypersaline environments and their biotechnological potential.

Halophiles	Genus	Isolated from	Hydrolytic enzymes production	Reference
Halophilic bacteria	<i>Halobacillus</i>	Great Salt Lake, Utah	Lipase, amylase and protease	[56]
	<i>Halomonas</i>	Howz Soltan Lake (Iran)	Amylase and protease	[57]
	<i>Salinibacter</i>	Saltern crystallizer ponds (Spain)	Protease, amylase and nuclease	[58]
	<i>Oceanobacillus</i>	Ulleung Basin of the East Sea, Korea	Lipase, amylase and xylanase	[59]
	<i>Marinococcus</i>	Marine solar saltern, Korea	Amylase, protease and DNase	[60]
	<i>Marinobacter</i>	Mediterranean Sea	Amylase, xylanase and DNase	[61]
	<i>Virgibacillus</i>	Arabal soil of west coast of Karnataka	Protease, amylase, lipase and gelatinase	[62]
	<i>Halovibrio</i>	Great Salt Lake, Utah	Pectinase, lipase and pulullanase	[63]
	<i>Planococcus</i>	Deep-sea sediments of Okinawa Trough (China)	Amylase, protease and DNase	[54]
	<i>Salinivibrio</i>	Hypersaline lake, Iran	Catalase, protease, amylase and DNase	[64]
Halophilic archaea	<i>Halobacterium</i>	Great Salt Lake, Utah	Protease, amylase and nuclease	[55]
	<i>Haloferax</i>	Himalatt salt lakes of the Algerian Sahara	Esterase, xylanase and inulinase	[53]
	<i>Halococcus</i>	Solar salterns of Orissa and West Bengal, India	Glutaminase, asparaginase, lipase and caseinase	[65]
	<i>Halolamina</i>	omso solar saltern, Korea	Esterase and caseinase	[66]
	<i>Natrinema</i>	Aibi salt lake, Xinjiang, China	Protease, lipase and amylase	[67]
	<i>Halalkalicoccus</i>		Esterase, lipase and caseinase	[68]
	<i>Haloarcula</i>	Great Salt Lake, Utah	Pectinase, protease and xylanase	[55]
	<i>Haloterrigena</i>	Himalatt salt lakes of the Algerian Sahara	Amylase, cellulase and esterase	[53]

and play a vital role in the plant development and health (Table 1 and Fig. 1). These microbes can be used as biopesticides, phytostimulators and biofertilizers to protect against different plant pathogens [47]. *Proteobacteria*, *Actinobacteria*, *Firmicutes* and *Bacteroidetes* are the dominant bacterial phyla detected in the phyllosphere of *Salsola*, *Populus* and *Arabidopsis* plants. *Pseudomonas*, *Aeromonas*, *Bacillus*, *Halobacillus*, *Sphingomonas*, *Halomonas* and *Methylobacterium* are the most dominant bacterial genera in the phyllosphere of *Salsola* and *Acacia* [48, 49].

Biotechnological potential of halophilic microorganisms

Halophiles maintain their internal ion concentration or osmotic balance by accumulating salts internally to

survive under extreme conditions [50, 51]. Mostly bacteria use two major groups of compatible solutes including polyols, sugars and amino acids derivatives to maintain their osmotic balance. Moderate halophilic bacteria such as *Halobacillus*, *Halomonas*, *Salinibacter*, *Oceanobacillus*, *Marinococcus*, *Virgibacillus*, *Halovibrio* and *Salinivibrio* produce a number of hydrolytic enzymes, e.g., protease, lipase, amylase, xylanase, cellulase and DNase (Table 1). These enzymes have diverse applications in agriculture, food, leather, detergents, and pharmaceutical industries [52–54]. Haloarchaea are mostly amino acid utilizing facultative aerobes which require a number of growth factors and slightly elevated temperatures (35–45°C) for optimal growth. *Halobacterium*, *Haloferax*, *Halococcus*, *Halolamina*, *Halalkalicoccus*, *Haloarcula* and *Haloterrigena* are members of Halobacteriaceae. These haloarchaea have some distinctive fea-

tures such as gas vesicles, purple membrane and red-orange carotenoids [50, 55]. These microorganisms have ability to hydrolyze starch, proteins, casein, gelatin and xylan (Table 1).

Role of halophyte microbiome in salinity tolerance

The rhizosphere and phyllosphere of halophyte are colonised by a wide range of microorganisms. The structure and composition of soil microbial communities varies with change in root exudate composition, plant developmental stage and abiotic factors or environmental conditions [69]. Plant microbiome plays a vital role in plant health and productivity (Fig. 2). Plant growth promoting bacteria residing in the rhizosphere or phyllosphere of halophytes enhance plant growth through different mechanisms such as production of phytohormones (Indole acetic acid, cytokinin), solubilization of minerals (P, Zn), nitrogen fixation and control of plant pathogens by production of siderophores and HCN [37, 70, 71]. Halophilic bacteria and archaea also play an important role in the bioremediation of contaminated soils by degradation of complex organic compounds and facilitating the process of phytoremediation [72, 73]. Progress in sequencing technologies and metadata analysis showed that plant-microbe interactions are regulated by different mechanisms through a complex network of signaling events and consequently alleviating the salinity stress.

Phytohormones production

Rhizobacteria regulate plant hormonal status by releasing a number of exogenous hormones that enables plants to survive under salt stress conditions [74]. These hormones include auxins, cytokinins, abscisic acid, gibberellins and ethylene. IAA (indole acetic acid) produced by rhizobacteria increases root growth directly by stimulating the cellular responses such as cell division and differentiation [27]. Inoculation of *Halobacillus*, *Bacillus* and *Pseudomonas* strains enhanced salt tolerance in crops (wheat, corn and sugarcane) and improved catalase and peroxidase activity, increased concentration of total soluble sugar contents and certain amino acids and K^+/Na^+ ratio [75]. Inoculation of cytokinin producing *Bacillus* strains increased shoot biomass

but showed a little effect on root biomass in lettuce seedlings under salt stress conditions. The cytokinin signaling in roots may be decreased due to production of abscisic acid in shoots [76, 77]. PGPR strains such as *Bacillus*, *Halobacillus*, *Micrococcus*, *Halomonas*, *Planococcus* and *Oceanobacillus* lowered the ethylene concentrations due the presence of enzyme ACC (1-aminocyclopropane-1-carboxylic acid) deaminase (Fig. 2). Rhizobacteria decreased the quantity of ACC outside the plant by the uptake and subsequent hydrolysis of ACC and maintain a balance between the internal and external ACC levels. These bacteria also decrease the inhibitory effect of ethylene on root elongation [78].

Exopolysaccharides matrix

Halotolerant and halophilic bacteria secrete exopolysaccharides (EPS) which are useful for attachment with root surfaces or soil particles (Fig. 2). They play important roles in plant-microbe interactions, cellular associations among microorganisms and protection of plant tissues against bacterial, viral and protists attack [79–81]. EPS are also involved in stabilization of soil structure and water holding capacity of soil particles. Inoculation of halophilic bacteria *Halomonas*, *Halobacillus* and *Planococcus* increased wheat, *Sesuvium* and chickpea growth under salinity stress conditions [82, 83].

Halocins

Halocins are the proteinaceous bacteriocins produced by extremely halophilic bacteria and archaea. Halocins have been classified into two types: (1) Microhalocins (peptides) which have size less than 10 kDa and (2) protein halocins which have size more than 10 kDa (Fig. 2). Their bactericidal modes of action have a wide range including DNA and RNA nuclease activity, inhibition of transcription and translation, pore formation and bacteriolysis [84–86]. All halobacteria and archaea are not sensitive to any particular halocins. Sensitive strains form a zone of inhibition on a double-agar overlay plate in response to the presence of halocins. Halocin H4 was the first halocins characterized from *Haloferax* sp. Halocin G1, R1, A2, H6, C8 and A4 are reported halocins and a few of them have been studied at the molecular level [87]. High throughput sequencing techniques showed that halocins positively affect the plate proteome and enhanced tolerance salinity of plants. Bacteriocin

thuricin 17 produced by *Bacillus thuriensis* differentially change the proteome of *Arabidopsis* under salinity stress conditions (200 mM NaCl). Some plant proteins involved in carbon and energy metabolism pathways are manipulated by bacterial signals [88].

Volatile organic compounds and polyamines

PGPR strains released volatile organic compounds that modulate salt and drought stresses and stimulate plant growth. Bacterial inoculation with *Bacillus*, *Pseudomonas* and *Halomonas* resulted in increased plant biomass of wheat, reduction in volatile emissions and higher rate photosynthesis [89]. *Bacillus subtilis* producing volatile compounds regulate the specific Na-related homeostasis in salt-stressed *Arabidopsis* [90]. These compounds mediate the plant homeostasis by increasing proline and chlorophyll and decreasing root Na⁺ accumulation (Fig. 2). Polyamines (PA) secreted by PGPR positively affect the osmotic stress in plants. Inoculation of *Bacillus megaterium* BOFC15 manipulate PA-mediated cell signaling and increased cellular polyamines in *Arabidopsis* that contributes to the osmotic stress in plants [91].

Halophyte adaptations

Salt tolerance in halophytes can be achieved by using two mechanisms, either by salt inclusion or salt exclusion. Halophytes utilize energy for the exclusion of excess salt from plant cells to protect themselves from toxic effects of high salinity [92]. Concentrations of Na⁺ and Cl⁻ ions in root and leaf cells are usually in the order of 11–30 mM. Na⁺/H⁺ antiporters form a proton gradient and its activity increase in halophytes with increase in salt concentrations [93]. Some halophytes can survive under saline conditions by using sequestration of salt to the vacuoles (Fig. 2). Cells in these plants have new vacuolar space fast enough to keep vacuolar salt concentration below a threshold value [94]. Halophytes also use small organic molecules (compatible solutes) such as trehalose, betaine, and proline to survive under salt stress conditions [95]. Compatible solutes can be classified according to their chemical nature; (1) anionic solutes, (2) zwitterionic solutes and (3) non-charged solutes. Some halophytes have special glands to secrete excessive salts from the plants (Fig. 2). These glands evapo-

rate water and cause crystallization of salts on leaf surface [96]. Some halophyte proteins, e.g., aquaporin is used for intracellular compartmentalization of the water (Fig. 2). These pore forming proteins control water movement in plant cells and play an important role in salt tolerance of halophytes [97].

Effect of host on the plant microbiome

Plant-microbe interactions are highly complex and dynamic. The plant immune system is usually triggered when they exposed to microorganisms. The response of plant to pathogenic microbes is called pathogen-associated molecular patterns (PAMPs) or PAMP-triggered immunity [98]. Microorganisms also evolve specific features such as secretion of chitin or flagellin through microbe-associated molecular patterns (MAMPs) [99]. Production of salicylic acid in the phyllosphere of *Arabidopsis thaliana* mediated the defense system and reduced the endophyte microbial diversity [24]. Plants produce a variety of signaling hormones to coordinate with different kinds of environmental factors or pathogens [100]. Degradation of plant hormones or precursor molecules by different plant-associated microbes, e.g, production of ACC deaminase by rhizobacteria prevents plant ethylene signaling and enhance plant ability to environmental stresses [35].

Some chemical signals produced by halophytes and some other plants facilitate the plant-microbe interactions such as strigolactones induce hyphal branching in mycorrhizal fungi, flavonoids mediate the microbial diversity in roots and other plant tissues [101, 102]. Some halophyte genes and pathways mediate the symbiosis relationship among plants and microorganisms, e.g., rhizobial and mycorrhizal symbiosis. Some plants produce alkaloids, terpenoids and phenolics to control pathogenic microorganisms [103]. *Avena sativa* (oat) produces avenacins which are well known triterpenoids with antifungal activity [104]. Microbial diversity analysis of transgenic maize (Bt-maize) and wild-type maize has shown no significant difference. This may be due to Bt-toxin is insecticidal rather than antibacterial [105, 106].

Halophytes have evolved complex mechanisms to tolerate soil salinity. Plant microbiome functions in a more sensitive and cost-effective manner to mediate the soil

salinity. Plant-associated microbes are key players in global biogeochemical cycles. Shifts in the microbial communities with increasing soil salinity has suggested that they play an important role in salt tolerance of plants. Halophilic and halotolerant PGPR strains contribute to salinity stress and enhance plant growth by production of phytohormones, biosynthesis of exopolysaccharides, ACC deaminase and volatile organic compounds. These organic molecules act as chemical signals for plant metabolic pathways, help to improve soil properties that reduce the adverse effects of soil salinity. Thus, halophilic and halotolerant PGPR strains can be used as biofertilizers and biocontrol agents to improve crop yield under salinity stress conditions.

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Conflict of Interest

The authors have no financial conflicts of interest to declare.

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