

Halotolerant Plant Growth Promoting Bacteria Mediated Salinity Stress Amelioration in Plants

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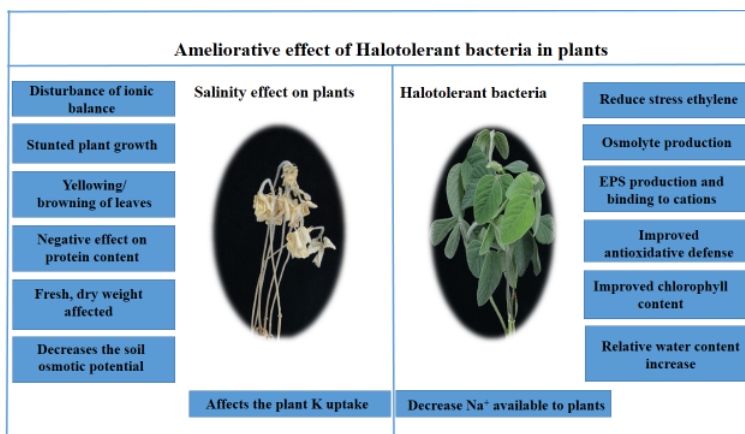
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Soil salinization refers to the buildup of salts in soil to a level toxic to plants. The major factors that contribute to soil salinity are the quality, the amount and the type of irrigation water used. The presented review discusses the different sources and causes of soil salinity. The effect of soil salinity on biological processes of plants is also discussed in detail. This is followed by a debate on the influence of salt on the nutrient uptake and growth of plants. Salinity decreases the soil osmotic potential and hinders water uptake by the plants. Soil salinity affects the plants K uptake, which plays a critical role in plant metabolism due to the high concentration of soluble sodium (Na^+) ions. Visual symptoms that appear in the plants as a result of salinity include stunted plant growth, marginal leaf necrosis and fruit distortions. Different strategies to ameliorate salt stress globally include breeding of salt tolerant cultivars, irrigation to leach excessive salt to improve soil physical and chemical properties. As part of an ecofriendly means to alleviate salt stress and an increasing considerable attention on this area, the review then focuses on the different plant growth promoting bacteria (PGPB) mediated mechanisms with a special emphasis on ACC deaminase producing bacteria. The various strategies adopted by PGPB to alleviate various stresses in plants include the production of different osmolytes, stress related phytohormones and production of molecules related to stress signaling such as bacterial 1-aminocyclopropane-1-carboxylate (ACC) derivatives. The use of PGPB with ACC deaminase producing trait could be effective in promoting plant growth in agricultural areas affected by different stresses including salt stress. Finally, the review ends with a discussion on the various PGPB activities and the potentiality of facultative halophilic/halotolerant PGPB in alleviating salt stress.

Key words: Soil salinity, Saline, Sodic, Saline-sodic, Plant growth promoting bacteria, 1-amino cyclopropane-1-carboxylate (ACC)



Effect of salt stress in plants and different strategies of amelioration by halotolerant bacteria.

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Introduction

Soil salinity is a severe problem affecting agricultural productivity in about 1/3rd of World's irrigated lands (Munns and Tester, 2008). Soil salinization is a worldwide land degradation process occurring in either arid and semi-arid regions as a result of natural or man process through irrigation (Mashmbye et al., 2012). In general soils are considered to be saline if they have concentration sufficient to interfere with the growth of most crop species (Bui, 2013). Though data pertaining to salt-affected areas vary, it is understood that about 7% of the earth's content equal to an area of about 1 billion hectare is affected by soil salinity (Ghassemi et al., 1995). In general soils are considered to be saline if they have concentration sufficient to interfere with the growth of most of crop species (Bui, 2013).

Soil salinity has its influence on plant growth and yield by direct or indirect effect. The accumulation of salts in the root zone affects plant growth due to its low osmotic potential, which exerts ion imbalance and ion toxicity and decrease the availability of water to the plants (Setia et al., 2013). Indirect influence includes its effect on the composition and activity of microbial community of soil (Chowdhury et al., 2011). The other effects of salt injury includes changes in the allocation pattern such as increased root at the expense of leaf growth (Brugnoli and Biorkman, 1992), decreased photosynthetic rate due to premature leaf senescence and partial stomatal closure and nutritive imbalance due to excessive Cl⁻ and Na⁺ in saline soils (Munns and Tester, 2008).

Various strategies involved to mitigate salt stress include: development of salt resistant cultivars, use of excessive irrigation to leach the salts from upper to lower soil depths, reduction of salt by harvesting salt accumulating aerial parts (Asada, 1992). Increased labor intensiveness and cultivation cost involved in the above mentioned methods have led to search for other viable alternatives and one such alternative is the user of plant growth promoting bacteria (PGPB) to alleviate salt stress, nowadays (Mayak et al., 2004). The use of bacteria to promote plant growth under different environmental conditions are reported by numerous workers (Kloepper et al., 1989; Glick and Bashan, 1997; Grichko and Glick, 2001; Mayak et al., 2004a,b; Zahir et al., 2009). Bacteria that improve health and yield of plant have been explored from the rhizosphere soil of different crop plants (Park et al., 2005; Ahmed et al., 2008; Duan et al., 2009), sewage sludge (Krause et al., 2003), milk (Das Gupta et al., 2006), cow dung (Swain et al., 2008) and insect gut (Indiragandhi et al., 2007), saline soil (Upadhyay et al., 2009), petroleum contaminated saline alkaline soil (Liu et al., 2009), and nickel contaminated soil (Durand et al., 2015).

PGPR promote plant growth by either direct or indirect mechanisms or a combination of both (Glick et al., 1998). Indirect mechanisms of plant growth include the pathogen

suppression through the action of siderophores, or the production of antibiotics or extra-cellular hydrolytic enzymes (Kloepper et al., 1989; Glick and Bashan, 1997). Direct mechanisms may include altered nutrition by provision of fixed nitrogen, iron through siderophores, soluble phosphate and Zn (Hariprasad and Niranjana, 2009; Iqbal et al., 2010); production of phytohormones such as indole-3-acetic acid (IAA), cytokinin and gibberellins (Madhaiyan et al., 2006; Kang et al., 2009) or by the activity of ACC deaminase. ACC deaminase is an enzyme that can lower plant ethylene levels, which are typically increased by a wide variety of environmental stress such as organic contaminants, salt stress, drought, flooding, heavy metals, and pathogen attack (Grichko and Glick, 2001; Indiragandhi et al., 2008; Reed and Glick, 2005; Cheng et al., 2007; Zahir et al., 2009).

This review deals with problems associated with salinity in plants, their impact in nutrient uptake and stress ethylene synthesis and the role of PGPB with 1-amino cyclopropane-1-carboxylate (ACC) deaminase in promoting plant growth under these conditions. The scope of this review also extends to the potential application of halotolerant ACC deaminase containing PGPB in agricultural lands affected by stress particularly salinization.

Soil salinity in Agriculture Salinity of soils and ground water is a serious land degradation problem, which is growing steadily in many parts of the world and it affects about 10% of the total land surface. This salt affected area is estimated to be 9000 * 10⁶ ha (Flowers, 2004) and the deterioration rate is about 2 × 10⁶ ha per year (~1%) (Shilpi et al., 2008), with a predicted rise of 50% of arable lands by the year 2050 (Ashraf, 1994). In addition, about 20% of the irrigated agricultural land that contributes more than 30% of global agricultural production (Hillel, 2000) is adversely affected by salinity every year (Ghassemi et al., 1995). At present, around 100 countries are affected by salinity-sodicity induced abiotic stress and this is one of the world's most serious problem in agriculture (Rueda-Puente et al., 2007).

Excess accumulation of salt leads to degradation of soil structure, deflocculation, prevalence of anaerobic conditions and increase in osmotic pressure, at the same time, water potential decreases, turgor potential of the cells (plant and microbes) declines and cells ultimately cease to grow. Microbial diversity, biomass and enzyme activity are severely inhibited in saline soils, which interferes with soil fertility and productivity becoming more acute in induced conditions (Tripathi et al., 2007; Ibekwe et al., 2010). In addition, salt stress also causes physiological drought, ion toxicity, nutrient imbalance, increased production of reactive oxygen species and stress ethylene level, resulting in decreased growth and premature activation of programmed cell death (PCD) (Feng et al., 2002; Mayak et al., 2004a; Jahromi et al., 2008). Production of ethylene by

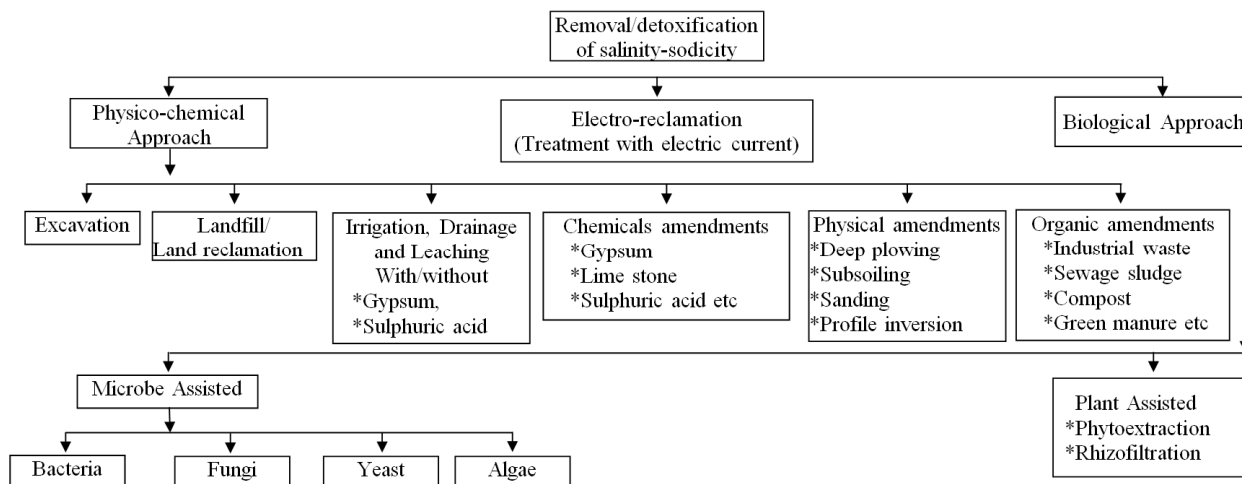


Fig. 1. Current approaches in the remediation of salinity-sodicity in salt affected soils.

Table 1. Classification of salt affected soils.

Classification	Electrical conductivity (dS m ⁻¹) ^a	Soil pH	Sodium adsorption ratio (SAR) ^b	Exchangeable sodium percentage (ESP)	Soil physical condition
Normal	<4.0	<13	6.5-7.51	<15 below	Good
Saline	>4.0	<8.5	<13	<15	Normal to poor
Sodic	<4.0	>8.5	>13	>15	Very poor
Saline-sodic	>4.0	<8.5	>13	>15	Poor

^adS m⁻¹ = mmho cm⁻¹.

^bIf reported as exchangeable sodium percentage (ESP), use 15% as threshold value.

Adapted and compiled from Bastida et al. (2008), Silvertooth (2001), Wong et al. (2008).

plant tissues significantly increases under salt stress and exacerbates leaf and petal abscission and organ senescence causing early death (Mayak et al., 2004a; Cheng et al., 2007) and this ethylene acts as a stress signaling molecule (Hahn and March, 2009).

Different strategies for management of salt affected soils including irrigation and drainage, leaching practices, soil aeration, physical, chemicals and organic amendments, electro-reclamation and biological treatments such as phytoremediation or use of plant-microbe interaction are being implemented (Qadir et al., 2000). The various approaches used for remediation of salinity-sodicity of soils are presented in Figure 1. The practice of adding soil amendments and irrigation-leaching strategy to ameliorate salt and sodic effects are profitable only, when good quality water and cheap chemicals are abundantly available. This also causes the loss of water, energy, essential nutrients, organic matter and deteriorates quality of ground water as well as neighboring water courses (Qadir et al., 2000). The rising cost of energy, poor quality of irrigation waters and inadequate resources for amendments of saline and sodic soil, demand the use of biological methods for reclamation of salt affected soil. Biological approaches considered for converting salt affected soils for agricultural use are: plant breeding, tissue culture, and genetic engineering,

which are long term and costly measures and beyond the economic means of developing nations (Cantrell and Linderman, 2001).

Saline soil: classification, causes of salinity and its effect on biological process Soil salinity is the measure of salt content in soil, taken by passing an electrical current through a soil solution extracted from soil sample (saturated) and the ability of this solution to carry current is called Electrical Conductivity (EC).

Classification of saline soils Typically, soil is slightly saline when the electrical conductivity of a soil 'saturation extract' is 4-8 dS m⁻¹, moderately saline at 8-16 dS m⁻¹, and strongly saline at more than 16 dS m⁻¹. But, EC alone cannot define the exact type/nature of the affected soil. United States Department of Agriculture (USDA) (1954) define salt affected soil as "saline, when EC is higher than 4 dS m⁻¹, and Salt Accumulation Ratio (SAR) and Exchangeable Sodium Percentage (ESP) are less than 13 and 15; saline-sodic when EC is greater than 4 dS m⁻¹, and SAR and ESP are greater than 13 and 15; and when EC is less than 4 dS m⁻¹, SAR and ESP greater than 13 and 15, the soil is sodic" (Table 1).

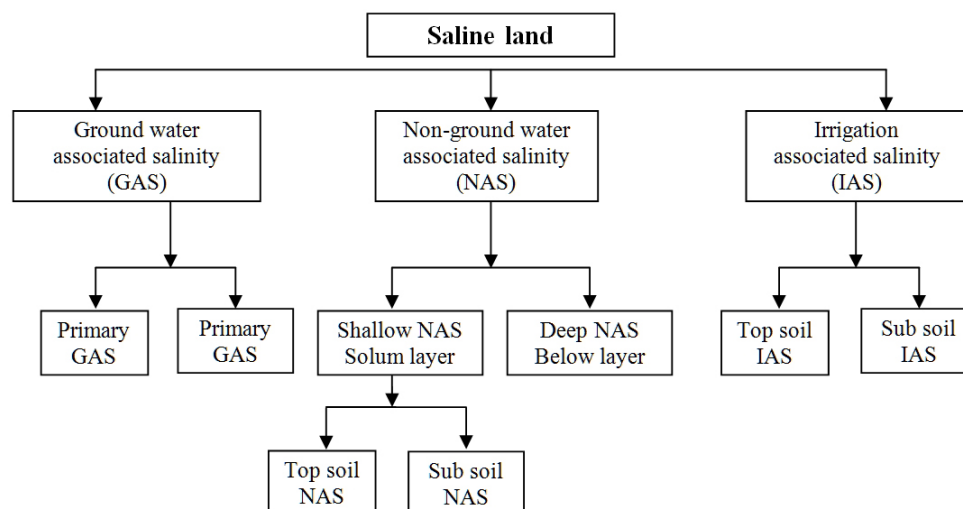


Fig. 2. Major types of salinity in world soils based on salinization processes (Rengasamy, 2006).

Sources and causes of soil salinization Soil Salinization is caused by natural processes, also known as primary salinization, and human-induced processes, known as secondary salinization (Ghassemi et al., 1995). Primary or natural causes of salinization results from gradual accumulation of weathering products of native rocks from fossil salts that are derived from prior deposits or from entrapped solutions found in earlier marine sediments (Spark, 1995). Secondary salinization will occur, where there is salt accumulation from poor quality irrigation water, rise of ground water level and the appearance of deep saline materials on the surface.

There are five major human activities that cause soil salinization: deforestation, construction of reservoirs, salt farming, irrigation using saline water, and lowering of land levels due to erosion and engineering works (Mitsuchi et al., 1986). The degrees of secondary salinization depend on climatic factors, geological factors and agricultural practices (Szabolcs, 1989). According to Rengasamy (2006), there are three major types of salinity (Figure 2) based on soil and ground water problem all over the world and these are different from the normal classification of 'Primary' or 'Secondary' salinity or saline and sodic soils as defined by Ghassemi et al. (1995). Briefly, (i) Groundwater associated salinity (GAS). In landscape discharge areas, water exits from the ground to the soil surface, which bring the salts dissolved in it. The driving force for upward movement of water and salts is evaporation from the soil plus plant transpiration. Salt accumulation is high when the water table is less than 1.5 m below the soil surface (Talsma, 1963). (ii) Non-groundwater-associated salinity (NAS). In landscapes where the water table is deep and drainage is poor, salts, which are introduced by rain, weathering, and kaeolian deposits, are stored within the soil solum. (iii) Irrigation associated salinity (IAS). Salts introduced by irrigation water are stored within the root zone because of insufficient leaching. Low hydraulic conductivity of soil

layers, poor quality irrigation water, as found in heavy clay soils and sodic soils, and high evaporative conditions accelerate irrigation-induced salinity. Approximately 950 million ha of land worldwide are estimated to be salt affected, with salinity affecting 23% of arable land and saline-sodic soils affecting a further 10% (Szabolcs, 1994). Salt affected soils (saline and sodic) are found in all continents. Tables 2, 3 and 4 show the worldwide distribution of salt affected soil.

Effects of salinization on biological processes of soil

Salinity-sodicity of soil has many harmful effects on soil

Table 2. Estimate of areas affected by secondary salinization in irrigated lands around the globe.

Country	Total land cropped Mha	Area irrigated		Area of irrigated land that is salt affected	
		Mha	%	Mha	%
China	97	45	46	6.7	15
India	169	42	25	7.0	17
Soviet Union	233	21	9	3.7	18
United states	190	18	10	4.2	23
Pakistan	21	16	78	4.2	26
Iran	15	6	39	1.7	30
Thailand	20	4	20	0.4	10
Egypt	3	3	100	0.9	33
Australia	47	2	4	0.2	9
Argentina	36	2	5	0.6	34
South Africa	13	1	9	0.1	9
Subtotal	843	159	19	29.6	20
World	1,474	227	15	45.4	20

Adapted and compiled from Ghassemi et al. (1995), Squires (2011).

Table 3. Regional distribution of salt affected soils, in million hectares (M ha).

Regions	Total area		Saline soils		Sodic soils	
	Mha	Mha	%	Mha	%	
Africa	1,899	39	2.0	34	1.8	
Asia, the pacific and Australia	3,107	195	6.3	249	8.0	
Europe	2,011	7	0.3	73	3.6	
Latin America	2,039	61	3.0	51	2.5	
Near East	1,802	92	5.1	14	0.8	
North America	1,924	5	0.2	15	0.8	
Total	12,781	397	3.1	434	3.4	

Adapted and compiled from Szabolcs, (1994), Ahemed et al. (2002), Rengasamy, 2006).

Table 4. Global distribution of saline and sodic soils.

Continent	Area (million hectares)		
	Saline	Sodic	Total
North America	6.2	9.6	15.8
Central America	2.0	-	2.0
South America	69.4	59.6	129.0
Africa	53.5	27.0	80.5
South Asia	83.3	1.8	85.1
North and Central Asia	91.6	120.1	211.7
Southeast Asia	20.0	-	20.0
Europe	7.8	22.9	30.7
Australasia	17.4	340.0	357.4
Total	351.5	581.0	932.2

*Adapted and compiled from Dregne and Chou (1992), Szabolcs (1994), IRR (2006).

chemical, physical properties and microbial processes. Osmotic stress from increased salinity limits microbial growth and activity (Oren, 1993). In addition, the toxicities of Na⁺ and other accompanying ions (e.g. Cl⁻ and CO₃²⁻), along with very high pH also inhibit microbial growth and activity (Zahran, 1997). Microorganisms in hypertonic environments (low water activity) either die or remain dormant, lowering the activity of various degrading enzymes released by microbes and eventually decreasing fertility (Tripathi et al., 2007; Egamberdieva et al., 2010). Pankhurst et al. (2001) reported that anthropogenic cause of salinity (non-saline soil), shift microbial community (non-halophiles) towards a less active and less diverse community. Whereas, coastal soils are natural habitat of halophilic/halotolerant bacteria. Halophilic bacteria (obligate halophiles) needs salt to grow and halotolerant bacteria (facultative halophiles) and can tolerate a wide range of salt concentration (Larsen, 1986; Yoon et al., 2003).

Mavi et al. (2012) reported that salinity will decrease the soil microbial activity due to decreased organic matter

decomposition and sodicity would increase microbial activity due to increased soil organic matter solubility. Pan et al. (2013) reported a decrease in organic C content, alkaline phosphatase, β-glucosidase, alkaline phosphatase and urease activities and an increase in available P concentration with an increase in salinity. Morrisey et al. (2014) reported that salinity increases the microbial decomposition rates and decrease the organic matter accumulation, carbon sequestration rates based on his studies conducted in lands with sea water intrusion.

Effects of salinization on plant growth Salinity has many harmful/negative effects on plant growth. Suitability of soils for crop production depends on the degree of salinity of the soil (Table 5). Salinity affects macro and micro nutrient uptake through competitive interactions with the major saline ions i.e., Na⁺ and Cl⁻, or by affecting soil reaction (pH) or ion selectivity of membrane transporters, such as the hydrogen-potassium transporter (*HKT1*) and the sodium overly sensitive (*SOS*). Grattan and Grieve (1992 and 1999) reported that high Na⁺ competitively induced Ca²⁺ and K⁺ deficiencies in plant. Salinity affects the uptake of these essential nutrients due to selectivity of the ion transporter (Marschner, 1995). Crop plants use K⁺ rather than Na⁺ as an important component of osmotic adjustment for maintenance of enzyme activity (Maser et al., 2002). However, K⁺ and Na⁺ compete for entry into plant cells because they have similar ionic radius and ion hydration energies (Schachtman and Liu, 1999) so that crops growing in saline soils may suffer from both Na⁺ toxicity and K⁺ deficiency. Decline in K⁺ accumulation due to salinity stress has been widely reported in sorghum (Netondo et al., 2004), Swiss chard (Hessini et al., 2005), barley (Jiang et al., 2006), and rice (Saleque et al., 2005). Macro nutrient Ca²⁺ and K⁺ are mobile and move from roots to shoots/leaves in plants grown under salt stress, partly protecting the plant from Na⁺ toxicity and reducing the effect of stress (Cramer, 2002).

Zhang et al. (2011) reported that high salinity lead to depletion in cellular water content and osmotic stress resulting in loss of yield. Jiang et al. (2013) reported that Na⁺ ions in excess stimulates ethylene induced tolerance mechanism based on his studies with *Arabidopsis thaliana* mutant. Rivero et al. (2014) reported that soil salinity affects Na⁺ and K⁺ uptake and osmoprotectant accumulation, and enzymes responsible for the accumulation observed under stress combination.

Possible PGPR mechanisms to enhance salt stress tolerance in plant Koul et al. (2015) reported a strong correlation between indole acetic acid (IAA) and Nitric oxide (NO) production in *A. brasilense* SM and suggested a possible existence of cross-talk or shared signaling mechanisms in growth regulators IAA and NO. Schlicht et al. (2013) reported coordinated release of NO and IAA from peroxisomes, which is behind the strong promotion of lateral root formation via

Table 5. Soil salinity classes and crop growth.

Soil salinity class	Conductivity of the saturation extract (dS m ⁻¹)	Effect on crop plants	Yield (%)
Non saline	0-2	Salinity effects negligible	100
Slightly saline	2-4	Yields of sensitive crops may be restricted	70-80
Moderately saline	4-8	Yields of many crops are restricted	40-70
Strongly saline	8-16	Only tolerant crops yield satisfactorily	0-40
Very strongly saline	>16	Only a few very tolerant crops yield satisfactorily	0

Adapted and compiled from Ayers and Westcot (1985), Salman et al. (2014).

indole-3-butyric acid (IBA). Bacterial osmolytes, such as glycine betaine act synergistically with plant osmolytes, accelerating osmotic adjustment. Proline synthesis, has shown increase in abiotic stressed plants in the presence of beneficial bacteria such as *Burkholderia* (Barka et al., 2006), as well as *Arthrobacter* and *Bacillus* (Sziderics et al., 2007); however, in pepper, proline also accumulated in the absence of abiotic stress in *Arthrobacter* and *Bacillus* treated plants, suggesting that these bacteria cause biotic stress on the pepper (Sziderics et al., 2007). Glycine-betaine produced by osmo-tolerant bacteria act synergistically with plant produced glycine-betaine in response to the stress, and this way, increase osmotic stress tolerance.

Plant-microbe interaction is a beneficial association between plants and microorganisms (Mayak et al., 2004a,b; Cheng et al., 2007) that provides a more efficient, cost effective and environment friendly method for the reclamation of salt affected soils and increase re-vegetation efficiency (in severely salt affected soil e.g. coastal soil) and crop production (in cultivated soil e.g. salinity induced by irrigation, soils in arid or semi-arid areas). The use of bacteria to promote plant growth under different environmental conditions and control plant pests (Kloepper et al., 1989; Glick and Bashan, 1997; Grichko and Glick, 2001; Mayak et al., 2004a,b; Zahir et al., 2009) continues to be an area of rapidly expanding research.

Another mechanism used by extremophiles is the secretion of exopolysaccharides (EPS). Extremophiles are organisms, such as halophiles and thermophiles that naturally live in extreme environments. Extremophile have novel metabolic pathways and might serve as sources of different polysaccharides (Hough and Danson, 1999). Bacterial exopolysaccharides (EPSs) lead to soil sheath development around the plant root, which reduces the flow of sodium into the stele. Geddie and Sutherland (1993) reported that EPSs produced by PGPB might bind cations including Na⁺ and decrease the amount of Na⁺ available for plant uptake, thus help alleviating salt stress in plants growing in saline environments.

Negative effect of salinity on plant growth is a consequence of salt stress induced stress levels of ethylene production (Mayak et al., 2004a; Cheng et al., 2007; Zahir et al., 2009). Bacterial hydrolysis of ACC leads to a decrease in plant

ethylene level, which, in turn, results in overall plant growth enhancement (Glick et al., 1998; Belimov et al., 2009). Mechanisms exerted by plant growth promoting bacterial strains in amelioration of salt stress is given in Table 6.

Bharti et al. (2013) investigated the inoculation of effect of three PGPB *Bacillus pumilus* STR2, *Halomonas desiderata* STR8 and *Exiguobacterium oxidotolerans* STR36, under 0, 100, 300 and 500 mM NaCl levels applied through irrigating water. These authors reported at 100 and 300 mM NaCl levels. *H. desiderata* inoculated plants recorded the highest herb yield, whereas at 500 mM NaCl, and *E. oxidotolerans* yielded maximum herb. Kang et al. (2014) evaluated the efficiency of PGPR strains *Burkholderia cepacia* SE4, *Promicromonospora* sp. SE188 and *Acinetobacter calcoaceticus* SE370 in reducing salinity stress in cucumber plants. These authors reported that the ameliorative effects of PGPR was evident by the increased water potential and decreased leakage of electrolyte leakage and these plants also have reduced sodium ion concentration, when compared to control under stress. Azarmi et al. (2015) reported that under salinity stress PGPR treatment efficiently enhanced proline concentration by 35 %, soluble sugars by 25 %, and reduced H₂O₂ levels by 18 % in the leaves and roots.

Role of ACC deaminase-producing PGPR in mitigation of salt stress

Since salinity stress boosts endogenous ethylene production in plants (Cuartero et al., 2005; Mayak et al., 2004a), reducing salinity-induced ethylene stress by any mechanism could likely decrease the negative impacts of salinity on plant growth. Recent studies have revealed that plants inoculated with PGPR containing ACC deaminase were able to thrive better through the salinity stress, while demonstrating a normal growth pattern. This, ameliorative effect was reported by Glick et al. (1997a,b) with inoculation of *P. putida* GR12-2 or its mutant *P. putida* GR12-2 acd68 on canola seedlings with/without stress. Likewise, this was reported by Mayak et al. (2004a) on ACC deaminase-producing *Achromobacter piechaudii* on tomato seedlings grown in the presence of NaCl (up to 172 mM). Saravanakumar and Samiyappan (2007) reported that *P. fluorescens* strain TDK1 containing ACC deaminase activity enhanced the saline resistance in groundnut plants and increased yield compared to

Table 6. Mechanism of salt stress tolerance in plants influenced by halotolerant bacterial inoculation.

Halotolerant PGPB	Crop	Salinity level	Mechanism	Reference
<i>Pseudomonas pseudoalcaligenes</i> ST1, <i>Bacillus pumilus</i> STR2	<i>Oryza sativa</i>	25 mM NaCl	Controlling caspase-like activity, programmed cell death, anti-oxidative activity	Jha et al. (2011)
<i>B. pumilus</i> STR2, <i>Exiguobacterium oxidotolerans</i> STR36	<i>Bacopa monneri</i> L.	4 g NaCl/Kg of soil	High proline content/lipid peroxidation	Bharati et al. (2012)
<i>Burkholderia phytofirmans</i> PsJN, <i>Enterobacter</i> sp. FD 17	<i>Zea Mays</i>	25 mM NaCl	Decreasing xylem Na ⁺ concentration/maintain nutrient balance within the plants	Akhtar et al. (2015)
Mixture of PGPR strains	<i>Vicia pannonica</i>	60 mM NaCl	Ameliorative effects due to mineral uptake, organic acid and hormone production	Esringu et al. (2015)
<i>P. putida</i> , <i>P. fluorescens</i> , <i>B. subtilis</i>	<i>Vicia faba</i>	40-80 mM NaCl	Modulating plant chlorophyll, protein and proline content	Metwali et al. (2015)
<i>B. pumilus</i> STR2, <i>Halomonas desiderata</i> STR8, <i>Exiguobacterium oxidotolerans</i> STR36	<i>Zea mays</i>	50 mM NaCl	Preventing major shifts indigenous microbial community	Bharti et al. (2015)
<i>P. putida</i> R4, <i>Pseudomonas chlororaphis</i> R5	<i>Corchorus olitorius</i> L.	0-75 mM NaCl	Synergistic interaction alleviated salt stress	Dilfuza and Jabborova (2015)
<i>Hartmannibacter diazotrophicus</i> E19 ^T	<i>Hordeum vulgare</i> L.	150 mM NaCl	Relative water content increase in the root system	Suarezet et al. (2015)
<i>P. simiae</i> strain AU-M4	<i>Glycine Max</i> L.	100 mM NaCl	Inoculated reduced Na ⁺ and enhanced K ⁺ uptake	Vaishnav et al. (2015)
<i>Acinetobacter</i> sp. ACMS25, <i>Bacillus</i> sp. PVMX4	<i>Phyllanthus amarus</i>	160 mM NaCl	Improved anti-oxidative defense system	Joe et al. (2016)
<i>P. fluorescens</i> 002	<i>Zea Mays</i>	150 mM NaCl	Improved root growth and root formation under salt stress	Zerrouk et al. (2016)
<i>Azotobacter chroococcum</i> AZ6	<i>Zea mays</i>	20mM NaCl	Improved chlorophyll a and total content, reduced proline and amino-acid content	Silinie et al. (2016)

Pseudomonas strains lacking ACC deaminase activity. Cheng et al. (2007) confirmed that ACC deaminase producing bacteria conferred salt tolerance to plants by lowering the synthesis of salt-induced stress ethylene and promoted the growth of canola in saline environment. Role of ACC deaminase containing halotolerant bacterial strains in inducing salt stress is given in Table 7.

Ali et al. (2014) reported that endophytes containing ACC deaminase can facilitate plant growth and development in the presence of salt stress. Endophytic *Pseudomonas fluorescens* YsS6, *P. migulae* 8R6 promoted plant growth under 165 mM and 185 mM NaCl stress. These authors reported that the plants pretreated with ACC deaminase containing bacterial endophytes exhibited higher biomass, chlorophyll contents, flowers and buds than the other treatments. Akhtar et al. (2014) subjected plants to combined treatment of biochar, ACC deaminase containing *Burkholderia phytofirmans* PsJN and *Enterobacter* sp. FD17 under salinity stress and reported that salinity significantly decreased the growth of maize, whereas both biochar and bacterial inoculation mitigated the negative effects of salinity

on maize. Kumari et al. (2016) reported that mutant strain AU-M4 obtained by treatment with N-methyl-N-nitro-N-nitrosoguanidine showed enhanced ACC deaminase activity, IAA production and P solubilization efficiency. Plant experiments conducted under salt stress revealed that both mutant and wild strain AU exhibited better tolerance against drought stress as evident by the higher plant biomass higher water content, proline accumulation and lower injury due to osmotic stress.

Factors influencing PGPB activities and potentiality of facultative halophilic/halotolerant bacteria as PGPB

Mayak et al. (2004a) reported that ACC deaminase-producing salt tolerant bacteria survive well and colonize under a saline environment and can help plants to overcome stress effect by their beneficial properties. Conversely, Upadhyay et al. (2009) showed that the performance of salt tolerant PGPB decreases with increasing salinity. Therefore, the most effective approach in developing efficient bio-inoculants would be to select microbes having multiple PGP activities that are highly

Table 7. Improvement of plant growth under salinity stress by ACC producing halotolerant bacteria.

Strain	Crop	Salinity	Plant growth promoting traits	Reference
<i>Pseudomonas fluorescens</i> strain TDK1	<i>Arachis hypogea</i>	120 mM NaCl	Salinity resistance in groundnut plants and improved yield	Saravanakumar and Samiyappan (2006)
<i>P. putida</i> N21 <i>P. aeruginosa</i> N39	<i>Triticum aestivum</i> L.	5-15 ds m ⁻¹ using NaCl	Improved plant height (52%), root length (60%) grain yield (76%) 100 grain weight (19%) straw yield (67%)	Zahir et al. (2009)
<i>P. fluorescens</i> PF169 <i>P. putida</i> PP108	<i>Brassica napus</i> L.	22 ds m ⁻¹ using NaCl and CaCl ₂	Improved seed germination and plant growth	Jalili et al. (2009)
<i>Bacillus aryabhatai</i> RS341, <i>Brevibacterium epidermis</i> RS15, <i>Micrococcus Yunnanensis</i> RS222	<i>Capsicum annuum</i> L.	150 mM NaCl	Ethylene production (47-64%), ACC concentration (47-55%) ACO activity (18-19%)	Siddikee et al. (2011)
<i>Achromobacter xylosoxidans</i> AUM54	<i>Catharanthus roseus</i>	50-150 mM NaCl	Decrease in stress ethylene level (11-23%), ascorbate peroxidase (19-32%), superoxide dismutase (20-30%) catalase (4-16%)	Karthikeyan et al. (2012)
<i>Raoultella planticola</i> ACTT33531	<i>Gossypium hirsutum</i> L.	Salt affected soil Xin jiung province china	Reduced ethylene and abscisic acid content in seedlings	Wu et al. (2012)
<i>Alcaligenes</i> sp.SBIACC2	<i>Oryza sativa</i>	150 mM NaCl	Improved germination, root and shoot growth and chlorophyll content	Bal et al. (2012)
<i>Bacillus</i> sp. KLBMP4941	<i>Limonium sinense</i>	100 and 200 mM NaCl	Enhanced germination percentage (81.8%), root length 159%, shoot length 131%, leaf area 87%	Qin et al. (2013)
<i>Brevibacterium epidermidis</i> RS15 <i>B. aryabhatai</i> RS341	<i>Brassica napus</i> L.	120 mM NaCl	Ethylene emission reduced by 35.4% (RS341) and 41.1% (RS515)	Sidikee et al. (2015)

adapted to particular soil environment. Since, halophilic and halotolerant bacteria naturally grow in saline environments and can grow in media containing wide range of NaCl (Yoon et al., 2003), the isolation of ACC deaminase-producing halotolerant bacteria should provide the best benefit for salt stressed plants.

Halophilic and halotolerant species live in areas such as hypersaline lakes, coastal dunes, saline deserts, salt marshes, and inland salt seas (Ramos-Cormenzana, 1993; Rodriguez-Valera, 1986). Halotolerant microorganisms possessed ability to grow in media without NaCl amendment and also in the presence of high NaCl concentration (Yoon et al., 2003). There are several categories of halotolerant microbes: non-tolerant, those which tolerate only a small concentration of salt (about 1% w/v); slightly tolerant, tolerating up to 6-8%; moderately tolerant, up to 18-20%; and extremely tolerant, those microbes that grow over the whole range of salt concentrations from zero up to saturation (Larsen, 1986) or according to Margesin and Schinner (2001) able to grow above approximately 15% (w/v) NaCl (2.5 M) are considered extremely halotolerant. *Bacillus clarkii*, *B. agaradhaerens* and *B. pseudofirmus* are some halotolerant bacteria isolated from soil were found to be tolerant up to 16% or 17% NaCl (Nielsen et al., 1995). Halophiles are a group of bacteria that require salt for growth,

non-halophilic, those that are often stimulated in their growth by a small amount of salt (1% of growth medium); slightly halophilic, grow optimally in the presence of 2-3% NaCl; moderately halophilic, grow best in the range of 5-10% NaCl (w/v); and extremely halophilic grow optimally at NaCl concentrations greater than 10% (w/v) (Larsen, 1986). *Haloarcula vallismortis* and *Haloterrigena turkmenica* for example, have been isolated from salt affected area of Death Valley, California, and saline soil of Turkmenia, respectively (Zvyagintseva and Tarasov, 1987) found to extremely halotolerant. Moderate halophiles are defined as those that grow optimally in media containing 3-15% (0.5-2.5 M) NaCl, such as *Halomonas maura* isolated from a saltern in Morocco, and *Marinococcus halophilus* isolated from sea sands (Bouchotroch et al., 2001; Hao et al., 1984) found to moderately halophilic.

Due to the capability of halotolerant bacteria to adapt to a wide range of salt concentrations, their potential applications to areas such as arid-zone agriculture, xeriscaping, aquaculture (of fish or algae), bio-production of desirable compounds (such as phycobiliproteins or carotenoids), or remediation of salt-affected soils, hold great promise. Some species of *Azospirillum*, a known terrestrial PGPB, are halotolerant (Hartmann and Zimmer, 1994) and survived in seawater, when

inoculated on mangrove seedling roots and promote growth (Puente et al., 1999). A number of ACC deaminase-producing mesophilic and salt tolerant PGPR isolated from various sources exhibited growth enhancing potentials in plants grown under various stresses including salt stress (Grickho and Glick, 2001; Mayak et al., 2004a; Zahir et al., 2009). Jha et al. (2011) reported that the strains *Brachybacterium saurashtrense* and *Pseudomonas* sp., showed better plant growth in *Salicornia* under salt stress conditions. Bharthi et al. (2016) reported improved plant growth of *Ocimum basilicum* CIM-Saumya plants applied with salt tolerant *Dietzia natronolimnaea* STR1, *Glomus intraradices* (Gi) and vermicompost under salt stressed soil conditions in greenhouse and field trials. Yaish et al. (2015) reported that the strains *Paenibacillus xylanexedens* PD-R6 and *Enterobacter cloacae* PD-P6 were able to enhance root elongation in canola grown under normal and saline conditions as evident by gnotobiotic root elongation assay. These bacteria can alter ethylene synthesis and IAA levels and can facilitate root nutrient uptake in date palm trees growing under salinity stress. Among these the re-mediation strategies, the use of PGPR mediated biological approach sounds as an effective, economical and long term solution to soil salinity.

Conclusion

Soil salinity has negative impact on plant growth, which in turn affects the yield and productivity in Agriculture. In this review the various source of soil salinity, the impact of soil salinity on soil health, crop yield and the approaches adapted for the reclamation of salt affected soils such as physico-chemical approaches, electro-reclamation and biological approaches are discussed in detail. It is assumed that the use of ACC deaminase-producing plant growth promoting halotolerant bacteria offer more advantages over other PGP bacteria because of their survival ability and stability of PGP attributes under saline environments. Halotolerant bacteria mediated salinity stress amelioration is also achieved by the production of bacterial osmolytes such as glycine betaine or through the production of EPS. The use of halotolerant ACC deaminase producing bacteria from salt affected areas has numerous advantages over its counterparts for effective salt stress mitigation. Thus halo-tolerant PGPR could be used environmental friendly and inexpensive strategy for better crop production and conservation in salt affected areas.

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