Plant Growth-Promoting Rhizobacteria and Salinity Stress: A Journey into the Soil

2

Bahman Fazeli-Nasab and R. Z. Sayyed

Abstract

A large number of studies have indicated that salinity stress and saline soils are cruel environmental limiting factors that retard the growth of crop plants. Present scenario of climate change will further increase the border of the area affected by saline soils, and therefore this phenomenon will threaten the productivity of crops leading to depletion of food sources of human societies. Various strategies including soil quality management policies, improving crop resistance against salinity stress, detoxification of noxious ions, improving the quality of irrigation water, and many other effects need to be examined to decrease the detrimental consequences associated with saline soils. In this context, the use of microorganisms especially plant growth-promoting rhizobacteria (PGPR) has been proposed as a sustainable way to fortify the quality of soils to help crop plants grow under salinity stress. Recent advances in molecular soil biology studies suggested that PGPR are involved in the important physiological process associated with plant growth and development. Among the other mechanisms, improvement in water and nutrient uptake, decrease in the toxicity of hazardous ions, amelioration of photosynthesis, improvement in nitrogen fixation, regulation/modulation of physiological signaling networks are the common features exhibited by PGPR to enhance the growth of plants in saline soils. Thus, it should be noted that these miracle bacterial species are *legendary soil guards* to protect both soil texture

B. Fazeli-Nasab (✉)
Research Department of Agronomy and Plant Breeding, Agricultural Research Institute, University of Zabol, Zabol, Iran
e-mail: Bfazeli@uoz.ac.ir

R. Z. Sayyed
Department of Microbiology, PSGVP Mandal's ASC College, Shahada, Maharashtra, India

R. Z. Sayyed et al. (eds.), *Plant Growth Promoting Rhizobacteria for Sustainable Stress Management*, Microorganisms for Sustainability 12,
https://doi.org/10.1007/978-981-13-6536-2_2

and crop plants from salinity stress in the light of present and upcoming global climate changes.

Keywords
PGPR · Salt stress · Phytohormones · Osmoregulation

2.1 Introduction

The upcoming global climate changes have drastically affected the productivity of crop plants. The increased weather temperature, an imbalance in CO_2 concentration, the delayed winter rainfall pattern, the drought stress, the modified micro- and macro-ecosystems, and more importantly soil salinity are the key issues associated with global climate changes. The constant erosion of the earth's crust causes the worldwide geological changes. The main, and perhaps most important, consequent associated with earth erosion is the exchange of soil ion contents. An enormous number of chemical compounds including sodium, calcium, chloride sulfate, carbonate, manganese, and other mineral and non-mineral elements are deformed or widely spread throughout the soil texture.

The presence of these elements in the soil will change the quality of soils (especially those are currently used to cultivate crop plants), and therefore they will lose their potential to provide water and nutritional elements for plants to grow (Amozadeh and Fazeli-Nasab 2012). In addition to the earth's crust erosion, the quality of irrigation water is another important factor to change the portion of toxic ions in soils. Many studies have reported that the excessive irrigation and poor/inadequate drainage are two factors that increase the salinity of soils (Ilangumaran and Smith 2017). Though the amount of stored salts in the soil structure is directly dependent on soil type, nonetheless the quality and quantity of water for irrigation can enhance the soil salinity by changing the total amount of ions present in each layer of soils (Phogat et al. 2018).

Normally, irrigation water contains 0.1–4 kg m^{-2} salt, and this amount of water is used annually in 1–1.5 m. So, an annual amount of 1–160 tons per hectare of salt is added to agricultural land. Irrigation water evaporates and its salts remain in the soil. For saltiness, these salts should be removed from the root area of the plants by leaching and drainage techniques. There is also evidence that farmers traditionally replaced resistant plants with susceptible plants, in dealing with the salinity problem. However, use of substitute plants to deal with salinity is likely to be used as a method for a long time before the leaching technique. Substitution of saline-resistant plants is used instead of susceptible plants in saline soils in the world. Some plants, such as sugar beet, barley, cotton, sugarcane, asparagus, and dates, have a high resistance to salinity (Kafi and Mahdavi-Damghani 2005).

The increasing demand for food production (especially for cereal plants) with a significant reduction in the use of chemical agents including herbicides, fungicides, pesticides, and synthetic fertilizers is a huge global concern to affect the future of agricultural systems. A huge number of scientific studies have reported that PGPR are environmental friendly microorganisms to increase the productivity of crop plants in modern agriculture epoch. In addition to their roles in the preparation of mineral and other chemical compounds for plant root system, they also exhibit their biological activities through direct and/or indirect interaction with other soil microorganisms to provide specific environment to fortify the growth of plants (Vejan et al. 2016). PGPR can protect plants from the harmful effects of pertaining to the environmental stresses including flooding, drought, salinity, heavy metals, and phytopathogens (Mayak et al. 2004; Yildirim et al. 2006) and also manage some of these operates through specific enzymes, which stimulate physiological changes in plants at the molecular level. Among these enzymes, ACC deaminase regulates plant hormones such as ethylene (Glick 2005; Arshad and Frankenberger 2012); on the other hand, PGPR stimulate plant growth through the activity of the enzyme ACC deaminase, which causes lower plant ethylene levels resulting in longer roots (Shah et al. 1998).

2.2 Salinity

Salinity is one of the major limiting factors that cause osmotic stress and decrease plant growth and crop productivity in arid and semiarid regions. In salinity process, increase in concentration of soluble salts in the root zone is one of the major complications, and also the rhizospheric populations affect the plant productivity (Cicek and Cakirlar 2002; Tank and Saraf 2010; Fazeli-Nasab 2018).

2.3 Adverse Effects of Salinity

2.3.1 Physiological and Morphological Disturbances

Salt stress reduces many aspects of plant metabolism like growth and yield. Salinity stress increases Na^+, which eventually decreases Ca^{2+} and K^+ (Yildirim et al. 2006). Accumulation of Na^+ can cause metabolic disturbances in some processes where Na^+ (low) and K^+ or Ca^{+2} (high) are required for optimal functioning and growth (Marschner 1995; Xu et al. 1999). The ability of cells to save salts is exhausted; salts build up in the intercellular space and then kill cells and organs (Sheldon et al. 2004). At higher status of available salt, the leaf area, size, and leaf production are reduced leading to the death of the plant (Suárez and Medina 2005).

2.3.2 Disturbances in Photosynthesis

Increasing salinity in the soil decreased some plant mechanisms like photosynthesis, chlorophyll content, and stomatal conductance, and all of these mechanisms will decrease photosynthetic capacity due to the osmotic stress and partial closure of stomata (Drew et al. 1990; Han and Lee 2005; Azad et al. 2017). Accumulation of Cl^- disrupts photosynthetic cycle.

2.3.3 Effects on Plant Growth and Crop Yield

Soil salinity limits plant growth and crop production in many parts of the world, particularly in arid and semiarid areas. However plants can suffer from membrane destabilization and general nutrient imbalance (Hasegawa et al. 2000; Parida and Das 2005). Plants after exposure by salt accumulate different molecules in their organics like proline, glucose, and glycine betaine.

Salinity tolerance can be defined by maintaining plant growth in an environment containing NaCl or a mixture of salts. Bray (1997) defined salt tolerance as having a negative effect on the growth of plants that store salt in their tissues, and also Maas and Hoffman classified crops into four groups on the basis of their tolerance to salinity: (i) relatively tolerant plants, (ii) resistant plants, (iii) semi-sensitive plants, and (iv) sensitive plants (Table 2.1).

2.3.4 Mechanisms to Combat Salinity Stress

Most of the salinity problems in higher plants are due to an increase in sodium chloride, which has spread to soils in the dry and coastal areas and their water resources. The high salinity of sodium chloride causes at least three types of problems in higher plants: (1) The osmotic pressure of the external solution results in an increase in the osmotic pressure of the plant cells, which requires osmotic regulation of the plant cells in order to avoid waste. (2) Removal and transfer of nutrients such as potassium and calcium ions are interrupted by excess sodium. (3) High levels of sodium and chlorine produce direct toxic effects on membrane and enzyme

Table 2.1 Grain tolerance to salinity in some important crops (Maas and Hoffman 1977)

Crop	Salinity level threshold $^{ds}/_{m}$	Crop	Salinity level threshold $^{ds}/_{m}$
(i) Relatively tolerant plants		**(ii) Resistant plants**	
Cowpea	4.9	Sugar beet	7
Soybean	5	Cotton	7.7
Wheat	6	Barley	8
Durum wheat	5.7	Chicken	6.9
Sorghum	6.8	Wheat grass	7.5
(iii) Semi-sensitive plants		**(iv) Sensitive plants**	
Alfalfa	2	Bean	1
Corn	1.7	Carrot	1
Rice	3	Orange	1.7
Tomato	2.5	Peach	1.7
Sugarcane	1.7	Apricot	1.6
Lettuce	1.3	Plum	1.5

systems. Osmotic stress is induced in plants under drought stress conditions, and since about 100 years ago, the term salinity stress is a form of physiological drought (Rengel 1992; Ding et al. 2018).

Some of the mechanisms for avoiding salinity are presence of small leaves to reduce transpiration, fewer stomata per leaf area, the presence of thick cuticle, and an increase in root-to-crown ratio. In the atmosphere, by regulating the osmotic content of sugars, the Na^+ and Cl^- levels are limited to the limb (Reich et al. 2017).

Resistance to salinity can be elevated through five major strategies:

1. Resistance to salinity in plants by improving traditional breeding and selection.
2. In the development of plants, along with their ancestors, they may acquire the trait of salinity resistance.
3. Farming of species that have salt tolerance (halophytes) can be identified, cloned, and inoculated by modification and selection for the development of their agronomic characteristics.
4. Salinity resistance genes.
5. Salinity-resistant plant growth-promoting rhizobacteria (Carter et al. 2012).

Plant growth responds to salinity in two stages: (1) a rapid stage (osmotic phase that inhibits growth of young leaves) and (2) a slower stage (ionic stage that accelerates senescence of mature leaves) (Munns and Tester 2008). The ability of plants-against salt condition is determined by several biochemical pathways that make easy retention and/or acquisition of water, protect chloroplast functions, and maintain ion homeostasis (Parida and Das 2005).

2.3.5 Production of Phytohormones

Studies have shown that indoleacetic acid and cytokinin are produced from amino acids such as tryptophan and adenine which secreted from the roots. Ethylene precursor is hydrolyzed to 1- amino cyclopropane, 2-carboxylic acid (1-aminocyclopropane-1-caboxylic, ACC) by enzyme ACC deaminase (Zahir et al. 2004). Activities of PGPR cause physiological changes in the morphology of the plant, and the set of these changes have a positive effect on growth, nutrition, and plant health.

2.3.6 Plant Hormones

2.3.6.1 Ethylene

The evolution of roots approximately 400 million years ago opened up the biological colonization of the land (Jackson 2017). Ethylene is a gaseous plant growth hormone produced endogenously by almost all plants and even in soil that plays a key role in inducing several physiological functions (Saleem et al. 2007).

The hormone ethylene also known as a stress hormone is released as a physiological response to different stresses such as edaphic and adaphic. Salinity can increase biosynthesis rate of ethylene via elevated levels of ACC, which may lead to physiological changes in plant tissues. Any check on this accelerated ethylene production in plants can improve growth of plants under salt stress (Hontzeas et al. 2004).

2.3.6.2 The Effect of Ethylene in Root Growth and Development

Ethylene was known as a stress hormone that is released by the plant as a physiological response when exposed to a different kind of stresses. It has been observed that plants inoculated with PGPR having ACC deaminase activity are more resistant to the deleterious effect of stress ethylene synthesized as a consequence of stress conditions (Penrose and Glick 2003; Zahir et al. 2004). Ethylene is of great importance in plant growth and development and also in some functions like inhibition of seed germination and root growth (Nordström and Eliasson 1984). As after germination, high level of ethylene would inhibit root elongation. Inhibition of the root elongation has been prevented due to inoculation of PGPR capable of containing ACC deaminase even in the presence of high (6%) concentration of salts, NaCl (Tank and Saraf 2010). PGPR inoculation helped in seed germination followed by lowering the plant's ethylene concentration, thereby decreasing the ethylene inhibition of seedling root length, while in many plants a burst of ethylene is required to break seed dormancy (Nascimento 2003).

2.3.6.3 Stress/Wound Ethylene

The term stress is used for an external factor capable of inducing a potentially injurious strain in living organisms. Stress ethylene is one of the general phenomena observed in plant tissues subjected to various unfavorable conditions (Hyodo 2017). Several kinds of stress are related to ACC such as effects of phytopathogenic bacteria and resistance to stress from polyaromatic hydrocarbons and from heavy metals (Glick et al. 2007). Plant seed inoculated with biocontrol bacteria strongly decreases plant diseases level and may help to protect fieldworkers from exposure to pathogens (Egamberdieva et al. 2008).

Bacterial strains containing ACC deaminase can, in part, at least alleviate the stress-induced ethylene-mediated negative impact on plants (Glick et al. 1998; Glick 2005; Safronova et al. 2006). It reported that ACC deaminase bacteria conferred salt tolerance onto plants by lowering the synthesis of salt-induced stress ethylene and promoted the growth of canola in the saline environment, and also it is related that in plants Cd is the strongest heavy element inductor of ethylene biosynthesis (Cheng et al. 2007).

Ethylene production in plants is induced by various environmental factors such as wounding, physical load, disease, drought, waterlogging, chilling temperature, and exposure to various chemicals (Hyodo 2017). There is evidence that treatment with aminoethoxy vinyl glycine (AVG) prevents ethylene inhibition of root elongation (Hall et al. 1996) and also ethylene inhibitors can decrease the negative effect and the expression of stress symptoms induced by ethylene in plants (Rost et al. 1986; Elad 1990).

2.3.6.4 ACC Deaminase and Its Biochemistry

Inoculation of PGPR in pepper, bean, canola, and lettuce under salt stress has been used for mitigating the effects of salinity. Reports also showed an improvement of squash plant when applied directly or as a transplant under salinity stress (Yildirim et al. 2006).

The enzyme ACC deaminase cleaves ethylene, and also for many plants a burst of ethylene is required to break seed dormancy and germination; however, higher levels of ethylene inhibits the root elongation (Ali-Soufi et al. 2017; Soni et al. 2018). Plants that are treated with ACC deaminase-producing PGPR have been shown to exhibit more resistant to the deleterious effects of stress ethylene synthesized as a consequence of stressful conditions such as flooding (Grichko and Glick 2001), heavy metals (Grichko et al. 2000), the presence of phytopathogens (Wang et al. 2000), drought, and high salt conditions (Penrose and Glick 2003).

The activity of ACC deaminase has been widely reported in different species of Gram-negative bacteria (Wang et al. 2000; Babalola et al. 2003), Gram-positive bacteria (Belimov et al. 2001; Ghosh et al. 2003)), rhizobia (Ma et al. 2003), endophytes (Pandey et al. 2005), and fungi (Jia et al. 1999). ACC deaminase is prevalent in different kinds of bacteria, viz., *Agrobacterium* and *Azospirillum* (Blaha et al. 2006), *Alcaligenes* and *Bacillus* (Belimov et al. 2001), *Burkholderia* (Blaha et al. 2006), *Enterobacter* (Penrose and Glick 2001), *Methylobacterium* (Madhaiyan et al. 2006), *Pseudomonas* (Belimov et al. 2001), *Ralstonia solanacearum* (Arshad and Frankenberger Jr 2012), *Rhizobium* (Ma et al. 2003), *Rhodococcus* (Stiens et al. 2006), *Sinorhizobium meliloti* (Belimov et al. 2001), and *Variovorax paradoxus* (Glick 2005). Owing to ACCD activity, these bacteria are known to help plant grow under biotic and abiotic stresses condition by decreasing the level of "stress ethylene" which is inhibitory to plant growth (Singh et al. 2015). The ACC deaminase enzyme produced by several rhizobacteria catalyzes and reduces the deleterious ethylene level (Soni et al. 2018) that acts as a sink for ACC and protects stressed plants from deleterious effects of stress ethylene (Glick 2005). Reports also showed that inoculation of plant with ACC deaminase containing PGPR has also resulted in enhanced chlorophyll contents of maize and lettuce (Han and Lee 2005; Tank and Saraf 2010).

The ability of a newly isolated ACC-utilizing bacterium, *Kluyvera ascorbata* SUD165, to improve the growth of canola, tomato, and Indian mustard seedlings treated with toxic concentrations of nickel, lead, and zinc has recently been demonstrated (Shah et al. 1998; Burd et al. 2000; Safronova et al. 2006).

2.4 Mechanisms of Salt Tolerance

2.4.1 Cytoplasmic Osmotic Regulation

Halophilic bacteria accumulate more salt in the protoplasm than those that are present in the external solvent medium through active ion harvesting; therefore, the intracellular water pressure remains negative in comparison with the external solution and its enzymatic systems evolved in a manner that is carried out under conditions of high salt levels in the protoplasm. Marine algae also use their own special organic solutions for osmotic regulation to keep their sodium cytoplasm concentration low (Ashraf and Wu 1994; Cao et al. 2017). One of the problems of salt stress is the reduction of the osmotic potential of the soil solution, so that the plant can absorb water from the soil. It should reduce the osmotic potential to less than the osmotic potential of the soil.

2.4.2 The Accumulation of Substances in Vacuole

Most of the high salinity plants accumulate sodium and potassium for osmotic regulation in vacuole. However, some grasses may also use organic solvents in vacuole (Srinivas et al. 2018). In this method, sodium transfer from cytoplasm to vacuole and also the return of potassium from vacuole to cytoplasm are performed by pumps. In this way, in addition to reducing the toxicity of sodium ion in the cytoplasm, the osmotic potential of the cell also decreases (due to the accumulation of salts in the vaccine), and this way the plant will be able to absorb water and salts from the soil. The mechanism of this problem is energy, that is, the transfer of sodium from the cytoplasm to the vaccine and the transfer of potassium from vaccine to cytoplasm with energy.

2.4.3 Absorption and Replacement of Ions

The first line of defense against the addition of excess sodium into the plant is the plasma membrane of the root cell, which has low sodium permeability in all studied species. Conversely, root cells have shown a high tendency to absorb potassium, which can accumulate unlike concentration slopes (Pitman et al. 1981; Mangalassery et al. 2017). Plants that tolerate low salinity under high concentration of sodium in the root environment show a significant reduction in potassium uptake and increase sodium uptake in the shoot (Rains 1969; Makhlouf et al. 2015).

2.4.4 Movement Paths Along the Root

Water and salts can enter the root through two paths of symplast and apoplasts. Symplast is through the cytoplasmic pathway of the root cells, which extends from the epidermis to the root of the brain and is related through the connections between the adjacent cells. Apoplasts transfer material through cell walls. Entering the symplast route is the most important control point for entering salt into the plant. The water entering the apoplastic pathway is more similar to that of the intracellular solution than with the solution outside the root, although the concentration of apoplastic salt can be corrected by absorbing into the cells along the path and by exchanging the ion walls of the cell (Tester and Davenport 2003; Reddy et al. 2017).

If the only route for the transfer of salts to the xylem is apoplastic pathway, air organs should be full of salt, however, the existence of a casparian strip makes this necessary that salts and water should pass through endoderm via the entrance of the symplastic system. It has been determined that thoracic plants often have a thick layer of cork, or dendritic cellulose cells have endoderm, while mesophytes often have a thin layer of casparian strip (Esashi 2017; Zarayneh et al. 2018).

2.4.5 Recovery of Sodium from Transpiration

When the water and soluble substances reach the root from the symplast they will be transfered from xylem to the air organs. Xylem parenchyma not only prevents the entrance of salts into the transpiration system, but also can reduce salts concentration in Sap via reabsorption of salts from transmitance of root to air oragns in transpiration system. The sodium in xylem is transmited to the Phloem in the base of stem by active transport which significantly reduces the amount of sodium in the transpiration. This conclusion was achived based on the experiments that aerial parts of the stem were wounded in a circular manner so that the phloem were disconnected but xylem left in a natural state. Then, Na^{22} was applied to the environment and it was observed that the plants with injured stem transmitted higher radioactive sodium to the leaves (about 84%) compared to the uninjured stems. Probably, the readsorbed salts are returned to the tip of the root inside the phloem (Gleason et al. 2017; Keisham et al. 2018).

2.4.6 Control of Salinity Levels in Leaves

The amount of salt in the transpiration pathway is lower than that of the extra-root solution even from salt accumulation pools, for example, barley, grown in 150 mM of NaCl in its transpiration pathway, has about 5 mM of sodium chloride (Rains 1969; Makhlouf et al. 2015). Rice, wheat, and barley have two adaptation methods to tolerate salts that reach the air organs – (1) salting by growth and (2) distribution of salts to older leaves – after the accumulation of salt in older leaves, they disappear, and thus the amount of salt in the plant decreases (Munns 1993; Sarabi et al. 2017).

2.4.7 Tubers and glandular trichomes

Susceptible plants often have specific methods for managing salt in the leaves. Examples of these mechanisms are the tubers and glandular trichomes for the removal of salts to the outer surfaces of the leaves. Salt glands are known in at least 11 plant families (10 dicotyledons and 1 cotyledon family, Gramminae). Salt tubers in gramminae contain two cells, one of which is base and the other is a warhead cell. Solar cells are collected by the base cell and driven out of the warhead cell. Both cells have dense cytoplasm with a large number of mitochondria and lack central vasculature. Anatomical sacks are distinguished from salt glands in the spinach family. Particularly in *Atriplex*, where all 200 species have salt bags that contain outburst cavities that include a long and narrow leg and a cell-like cell at the top of the epidermis, different species of *Atriplex* can be identified from the shape of their salt bags. The salt solution is transmited from mesophilic cells to glandular trichomes through stem cells agianst the gradient concentration. The salt accumulates in the central vacuolic glandular trichomes, which is eventually torn and is released at the surface of the leaf. Accumulated salts in the surface of the leaf may reduce transpiration and increase light reflection; more than 80% sodium chloride entering the Atriplex leaves may be removed through glandular trichomes (Akbar et al. 1972; Hairmansis et al. 2017).

2.4.8 Broiling to Regulate Osmotic Pressure in Leaves

All salt-tolerating plants are not able to excrete salts. Many salinity-resistant and nonsaline plants tolerate temporary increase of salt in apoplasts by increasing the amount of mesophilic cell water and therefore dilutes the salts and increases their capacity to absorb the salt from the apoplast solution (Kramer 1984; Joshi et al. 2015).

2.5 Conclusion

The salinity stress and saline soils are cruel factors that adversely affect the growth of crop plants leading to decrease in agriculture productivity and hence depletion of food sources of human societies. Salinity is one of the major limiting factors that cause osmotic stress and decrease plant growth and crop productivity in arid and semiarid regions. Salt stress reduces many aspects of plant metabolism like growth and yield. Most of the salinity problems in higher plants are due to an increase in sodium chloride which has spread to soils in the dry and coastal areas and their water resources. More importantly salinity in the soil decreases plant mechanisms like photosynthesis, chlorophyll content, stomatal conductance, membrane destabilization, and general nutrient imbalance. To mitigate the salinity, many strategies including soil quality management policies, use of saline resistance varieties, detoxification of noxious ions, improvement in the quality of irrigation water etc. have been in practice. However all these strategies pose limitations and are not sustainable; in this context, the use of microorganisms especially PGPR has been proposed as a sustainable and eco-friendly way to fortify the quality of soils to help crop plants grow under salinity stress. PGPR are involved in the important physiological process associated with plant growth and development under salinity. Among the various strategies adopted to elevate salinity use of halophilic, PGPR seems to be the best alternatives. PGPR elevate salinity or exhibit tolerance to salinity through the regulation of production of stress hormone ethylene under the influence of ACC deaminase, osmotic regulation, and accumulation of salts in their cytoplasm and absorption and replacement of ions. PGPR are responsible for increasing nutrient uptake, decreasing the toxicity of hazardous ions, amelioration of photosynthesis, improvement in nitrogen fixation, regulation/modulation of physiological signaling networks, etc. These miracle bacterial species are *legendary soil guards* to protect both soil texture and crop plants from salinity stress.

References

Akbar M, Yabuno T, Nakao S (1972) Breeding for saline-resistant varieties of rice: I. variability for salt tolerance among some rice varieties. Jpn J Breed 22(5):277–284

Ali-Soufi M, Shahriari A, Shirmohammadi E, Fazeli-Nasab B (2017) Seasonal changes biological characteristics of airborne dust in Sistan plain, Eastern Iran. In: Proceedings of the International Conference on Loess Research. Gorgan University of Agricultural Sciences and Natural Resources, Gorgan. https://www.researchgate.net/publication/326984018_Seasonal_changes_biological_characteristics_of_airborne_dust_in_Sistan_plain_Eastern_Iran

Amozadeh S, Fazeli-Nasab B (2012) Improvements methods and mechanisms to salinity tolerance in agricultural crops. In: Proceedings of the first national agricultural conference in difficult environments. Islamic Azad University, Ramhormoz Branch

Arshad M, Frankenberger WT Jr (2012) Ethylene: agricultural sources and applications. Springer Science & Business Media, New York. ISBN: 1461506751

Ashraf M, Wu L (1994) Breeding for salinity tolerance in plants. Crit Rev Plant Sci 13(1):17–42

Azad H, Fazeli-Nasab B, Sobhanizade A (2017) A study into the effect of Jasmonic and humic acids on some germination characteristics of Roselle (*Hibiscus sabdariffa*) seed under salinity stress. Iran J Seed Res 4(1):1–18. http://yujs.yu.ac.ir/jisr/article-1-235-fa.html. https://doi.org/10.29252/yujs.4.1.1

Babalola OO, Osir EO, Sanni AI, Odhiambo GD, Bulimo WD (2003) Amplification of 1-amino-cyclopropane-1-carboxylic (ACC) deaminase from plant growth promoting *rhizobacteria* in Striga-infested soil. Afr J Biotechnol 2(6):157–160

Belimov AA, Safronova VI, Sergeyeva TA, Egorova TN, Matveyeva VA, Tsyganov VE, Borisov AY, Tikhonovich IA, Kluge C, Preisfeld A (2001) Characterization of plant growth promoting *rhizobacteria* isolated from polluted soils and containing 1-aminocyclopropane-1-carboxylate deaminase. Can J Microbiol 47(7):642–652

Blaha D, Prigent-Combaret C, Mirza MS, Moënne-Loccoz Y (2006) Phylogeny of the 1-aminocyclopropane-1-carboxylic acid deaminase-encoding gene acdS in phytobeneficial and pathogenic Proteobacteria and relation with strain biogeography. FEMS Microbiol Ecol 56(3):455–470

Bray EA (1997) Plant responses to water deficit. Trends Plant Sci 2(2):48–54

Burd GI, Dixon DG, Glick BR (2000) Plant growth-promoting bacteria that decrease heavy metal toxicity in plants. Can J Microbiol 46(3):237–245

Cao D, Li Y, Liu B, Kong F, Tran LSP (2017) Adaptive mechanisms of soybean grown on salt-affected soils. Land Degrad Dev 29(4):1054–1064. https://doi.org/10.1002/ldr.2754

Carter D L, Chapman V, Doneen L, Kylin A, Peck A, Quatrano S, Shainberg I, Thomson W (2012) Plants in saline environments. Springer Science & Business Media. ISBN: 3642809294

Cheng Z, Park E, Glick BR (2007) 1-Aminocyclopropane-1-carboxylate deaminase from *Pseudomonas putida* UW4 facilitates the growth of canola in the presence of salt. Can J Microbiol 53(7):912–918

Cicek N, Cakirlar H (2002) The effect of salinity on some physiological parameters in two maize cultivars. Bulg J Plant Physiol 28(1–2):66–74

Ding W, Clode PL, Clements JC, Lambers H (2018) Effects of calcium and its interaction with phosphorus on the nutrient status and growth of three Lupinus species. Physiol Plant 163(3):386–398. PMID: 29570221. https://doi.org/10.1111/ppl.12732

Drew MC, Hold PS, Picchioni GA (1990) Inhibition by NaCl of net CO2 fixation and yield of cucumber. J Am Soc Hortic Sci 115(3):472–477
Egamberdieva D, Kamilova F, Validov S, Gafurova L, Kucharova Z, Lugtenberg B (2008) High incidence of plant growth-stimulating bacteria associated with the rhizosphere of wheat grown on salinated soil in Uzbekistan. Environ Microbiol 10(1):1–9
Elad Y (1990) Production of ethylene by tissues of tomato, pepper, French-bean and cucumber in response to infection by *Botrytis cinerea*. Physiol Mol Plant Pathol 36(4):277–287
Esashi Y (2017) Ethylene and seed germination. In: The plant hormone ethylene. CRC Press, pp 133–157
Fazeli-Nasab B (2018) The effect of explant, BAP and 2,4-D on callus induction of *trachyspermum ammi*. Potravinarstvo Slovak J Food Sci 12(1):578–586. https://doi.org/10.5219/953
Ghosh S, Penterman JN, Little RD, Chavez R, Glick BR (2003) Three newly isolated plant growth-promoting *bacilli facilitate* the seedling growth of canola, *Brassica campestris*. Plant Physiol Biochem 41(3):277–281
Gleason SM, Wiggans DR, Bliss CA, Young JS, Cooper M, Willi KR, Comas LH (2017) Embolized stems recover overnight in *Zea mays*: the role of soil water, root pressure, and nighttime transpiration. Front Plant Sci 8:662
Glick BR (2005) Modulation of plant ethylene levels by the bacterial enzyme ACC deaminase. FEMS Microbiol Lett 251(1):1–7
Glick BR, Penrose DM, Li J (1998) A model for the lowering of plant ethylene concentrations by plant growth-promoting bacteria. J Theor Biol 190(1):63–68
Glick BR, Cheng Z, Czarny J, Duan J (2007) Promotion of plant growth by ACC deaminase-producing soil bacteria. Eur J Plant Pathol 119(3):329–339
Grichko VP, Glick BR (2001) Amelioration of flooding stress by ACC deaminase-containing plant growth-promoting bacteria. Plant Physiol Biochem 39(1):11–17
Grichko VP, Filby B, Glick BR (2000) Increased ability of transgenic plants expressing the bacterial enzyme ACC deaminase to accumulate Cd, Co, Cu, Ni, Pb, and Zn. J Biotechnol 81(1):45–53
Hairmansis A, Nafisah N, Jamil A (2017) Towards developing salinity tolerant rice adaptable for coastal regions in Indonesia. KnE Life Sci 2(6):72–79
Hall JA, Peirson D, Ghosh S, Glick B (1996) Root elongation in various agronomic crops by the plant growth promoting *rhizobacterium Pseudomonas* putida GR12–2. Isr J Plant Sci 44(1):37–42
Han H, Lee K (2005) Plant growth promoting *rhizobacteria* effect on antioxidant status, photosynthesis, mineral uptake and growth of lettuce under soil salinity. Res J Agric Biol Sci 1(3):210–215
Hasegawa PM, Bressan RA, Zhu J-K, Bohnert HJ (2000) Plant cellular and molecular responses to high salinity. Annu Rev Plant Biol 51(1):463–499
Hontzeas N, Saleh SS, Glick BR (2004) Changes in gene expression in canola roots induced by ACC-deaminase-containing plant-growth-promoting bacteria. Mol Plant-Microbe Interact 17(8):865–871
Hyodo H (2017) Stress/wound ethylene. In: The plant hormone ethylene. CRC Press, pp 43–63
Ilangumaran G, Smith DL (2017) Plant growth promoting rhizobacteria in amelioration of salinity stress: a systems biology perspective. Front Plant Sci 8:1768. https://doi.org/10.3389/fpls.2017.01768
Jackson MB (2017) Ethylene in root growth and development. In: The plant hormone ethylene. CRC Press, pp 159–181
Jia Y-J, Kakuta Y, Sugawara M, Igarashi T, Oki N, Kisaki M, Shoji T, Kanetuna Y, Horita T, Matsui H (1999) Synthesis and degradation of 1-aminocyclopropane-1-carboxylic acid by *Penicillium citrinum*. Biosci Biotechnol Biochem 63(3):542–549
Joshi R, Mangu VR, Bedre R, Sanchez L, Pilcher W, Zandkarimi H, Baisakh N (2015) Salt adaptation mechanisms of halophytes: improvement of salt tolerance in crop plants. In: Elucidation of abiotic stress signaling in plants. Springer, New York, pp 243–279
Kafi M, Mahdavi-damghani A (2005) Mechanisms of plant resistance to environmental stresses (translation). Ferdowsi University of Mashhad. ISBN: 9789645782038

Keisham M, Mukherjee S, Bhatla SC (2018) Mechanisms of sodium transport in plants—progresses and challenges. Int J Mol Sci 19(3):647
Kramer D (1984) Cytological aspects of salt tolerance in higher plants. In: Salinity tolerance in plants. Wiley, New York, pp 3–16
Ma W, Sebestianova SB, Sebestian J, Burd GI, Guinel FC, Glick BR (2003) Prevalence of 1-aminocyclopropane-1-carboxylate deaminase in *Rhizobium* spp. Antonie Van Leeuwenhoek 83(3):285–291
Maas EV, Hoffman GJ (1977) Crop salt tolerance–current assessment. J Irrig Drain Div 103(2):115–134
Madhaiyan M, Poonguzhali S, Ryu J, Sa T (2006) Regulation of ethylene levels in canola (*Brassica campestris*) by 1-aminocyclopropane-1-carboxylate deaminase-containing *Methylobacterium fujisawaense*. Planta 224(2):268–278
Makhlouf K, Hamrouni L, Khouja M, Hanana M (2015) Salinity effects on germination, growth and mineral nutrition of *Ricinus communis* seedlings. Acta Bot Hungar 57(3–4):383–400
Mangalassery S, Dayal D, Kumar A, Bhatt K, Nakar R, Kumar A, Singh J, Misra AK (2017) Pattern of salt accumulation and its impact on salinity tolerance in two halophyte grasses in extreme saline desert in India. Indian J Exp Biol 55(8):542–548
Marschner H (1995) Mineral nutrition of higher plants, 2nd edn. Academic, London
Mayak S, Tirosh T, Glick BR (2004) Plant growth-promoting bacteria that confer resistance to water stress in tomatoes and peppers. Plant Sci 166(2):525–530
Munns R (1993) Physiological processes limiting plant growth in saline soils: some dogmas and hypotheses. Plant Cell Environ 16(1):15–24
Munns R, Tester M (2008) Mechanisms of salinity tolerance. Annu Rev Plant Biol 59:651–681. https://doi.org/10.1146/annurev.arplant.59.032607.092911
Nascimento WM (2003) Ethylene and lettuce seed germination. Sci Agric 60(3):601–606. https://doi.org/10.1590/S0103-90162003000300029
Nordström AC, Eliasson L (1984) Regulation of root formation by auxin-ethylene interaction in pea stem cuttings. Physiol Plant 61(2):298–302
Pandey P, Kang S, Maheshwari D (2005) Isolation of endophytic plant growth promoting Burkholderia sp. MSSP from root nodules of *Mimosa pudica*. Curr Sci 89:177–180
Parida AK, Das AB (2005) Salt tolerance and salinity effects on plants: a review. Ecotoxicol Environ Saf 60(3):324–349. https://doi.org/10.1016/j.ecoenv.2004.06.010
Penrose DM, Glick BR (2001) Levels of ACC and related compounds in exudate and extracts of canola seeds treated with ACC deaminase-containing plant growth-promoting bacteria. Can J Microbiol 47(4):368–372
Penrose DM, Glick BR (2003) Methods for isolating and characterizing ACC deaminase-containing plant growth-promoting *rhizobacteria*. Physiol Plant 118(1):10–15
Phogat V, Pitt T, Cox J, Šimůnek J, Skewes M (2018) Soil water and salinity dynamics under sprinkler irrigated almond exposed to a varied salinity stress at different growth stages. Agric Water Manag 201:70–82. https://doi.org/10.1016/j.agwat.2018.01.018
Pitman MG, Läuchli A, Stelzer R (1981) Ion distribution in roots of barley seedlings measured by electron probe X-ray microanalysis. Plant Physiol 68(3):673–679
Rains DW (1969) Sodium and potassium absorption by bean stem tissue. Plant Physiol 44(4):547–554
Reddy INBL, Kim B-K, Yoon I-S, Kim K-H, Kwon T-R (2017) Salt tolerance in rice: focus on mechanisms and approaches. Rice Sci 24(3):123–144
Reich M, Aghajanzadeh T, Helm J, Parmar S, Hawkesford MJ, De Kok LJ (2017) Chloride and sulfate salinity differently affect biomass, mineral nutrient composition and expression of sulfate transport and assimilation genes in *Brassica rapa*. Plant Soil 411(1–2):319–332
Rengel Z (1992) The role of calcium in salt toxicity. Plant Cell Environ 15(6):625–632
Rost T, Jones T, Robbins J (1986) The role of ethylene in the control of cell division in cultured pea root tips: a mechanism to explain the excision effect. Protoplasma 130(1):68–72

Safronova VI, Stepanok VV, Engqvist GL, Alekseyev YV, Belimov AA (2006) Root-associated bacteria containing 1-aminocyclopropane-1-carboxylate deaminase improve growth and nutrient uptake by pea genotypes cultivated in cadmium supplemented soil. Biol Fertil Soils 42(3):267–272

Saleem M, Arshad M, Hussain S, Bhatti AS (2007) Perspective of plant growth promoting rhizobacteria (PGPR) containing ACC deaminase in stress agriculture. J Ind Microbiol Biotechnol 34(10):635–648

Sarabi B, Bolandnazar S, Ghaderi N, Ghashghaie J (2017) Genotypic differences in physiological and biochemical responses to salinity stress in melon (*Cucumis melo* L.) plants: prospects for selection of salt tolerant landraces. Plant Physiol Biochem 119:294–311

Shah S, Li J, Moffatt BA, Glick BR (1998) Isolation and characterization of ACC deaminase genes from two different plant growth-promoting *rhizobacteria*. Can J Microbiol 44(9):833–843

Sheldon A, Menzies N, So HB, Dalal R (2004) The effect of salinity on plant available water. SuperSoil. 2004 418(1–2):477–491. https://doi.org/10.1007/s11104-017-3309-7

Singh RP, Shelke GM, Kumar A, Jha PN (2015) Biochemistry and genetics of ACC deaminase: a weapon to "stress ethylene" produced in plants. Front Microbiol 6:937. PMID: 26441873, PMCID: PMC4563596. https://doi.org/10.3389/fmicb.2015.00937

Soni R, Yadav SK, Rajput AS (2018) ACC-deaminase producing *rhizobacteria*: prospects and application as stress busters for stressed agriculture. In: Microorganisms for green revolution. Springer, Singapore, pp 161–175

Srinivas A, Rajasheker G, Jawahar G, Devineni PL, Parveda M, Kumar SA, Kishor PBK (2018) Deploying mechanisms adapted by halophytes to improve salinity tolerance in crop plants: focus on anatomical features, stomatal attributes, and water use efficiency. In: Salinity responses and tolerance in plants, vol 1. Springer, Cham, pp 41–64

Stiens M, Schneiker S, Keller M, Kuhn S, Pühler A, Schlüter A (2006) Sequence analysis of the 144-kilobase accessory plasmid pSmeSM11a, isolated from a dominant *Sinorhizobium meliloti* strain identified during a long-term field release experiment. Appl Environ Microbiol 72(5):3662–3672

Suárez N, Medina E (2005) Salinity effect on plant growth and leaf demography of the *Mangrove Avicennia germinans* L. Trees 19(6):721–727

Tank N, Saraf M (2010) Salinity-resistant plant growth promoting *rhizobacteria ameliorates* sodium chloride stress on tomato plants. J Plant Interact 5(1):51–58

Tester M, Davenport R (2003) Na^+ tolerance and Na^+ transport in higher plants. Ann Bot 91(5):503–527

Vejan P, Abdullah R, Khadiran T, Ismail S, Nasrulhaq Boyce A (2016) Role of plant growth promoting rhizobacteria in agricultural sustainability—a review. Molecules 21(5):573. https://doi.org/10.3390/molecules21050573

Wang C, Knill E, Glick BR, Défago G (2000) Effect of transferring 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase genes into *Pseudomonas fluorescens* strain CHA0 and its gac A derivative CHA96 on their growth-promoting and disease-suppressive capacities. Can J Microbiol 46(10):898–907

Xu G, Magen H, Tarchitzky J, Kafkafi U (1999) Advances in chloride nutrition of plants. Adv Agron:97–150. Elsevier

Yildirim E, Taylor A, Spittler T (2006) Ameliorative effects of biological treatments on growth of squash plants under salt stress. Sci Hortic 111(1):1–6

Zahir ZA, Arshad M, Frankenberger WT (2004) Plant growth promoting rhizobacteria: applications and perspectives in agriculture. Adv Agron 8:198–169

Zarayneh S, Sepahi AA, Jonoobi M, Rasouli H (2018) Comparative antibacterial effects of cellulose nanofiber, chitosan nanofiber, chitosan/cellulose combination and chitosan alone against bacterial contamination of Iranian banknotes. Int J Biol Macromol 118:1045–1054. https://doi.org/10.1016/j.ijbiomac.2018.06.160