Chapter 5
Plant Growth Promotion by ACC Deaminase-Producing Bacilli Under Salt Stress Conditions

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5.1 Introduction

Agriculture is a dominant activity in worldwide economic, social, and environmental development, contributing to 80% of the food consumed globally (FAO 2018). However, this activity around the world faces several soil adversities, which can negatively impact food production, causing economic losses to producers. Soil degradation in agroecosystems is a serious problem that tends to be ignored, even when it has accelerated rates around the world (Borrelli et al., 2015; Dotterweich, 2013; Ligonja and Shrestha 2015). This event has negative impacts on the future of food safety by reducing soil fertility, which causes biotic and abiotic stress for crops (Dercon et al. 2012). Some examples of abiotic stress include extreme environmental conditions, such as high or low temperatures or pH, low nutrient availability in soils, flooding, prolonged periods of drought, and high concentrations of metals and salts (Glick 2014; Santoyo et al. 2016). Among them, salinity in soils is recognized as one of the factors that most affect agricultural production, and it is estimated that 20% of cultivated areas are affected by this stress condition (Flowers 2004). For

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example, salinity has caused a loss of about 65% of wheat yield in moderately saline soils (Shafi et al. 2010); due to that abiotic stress affects almost all aspects of plant development including germination, vegetative growth, and reproductive development (Foolad 2004). Thus, the global food production is negatively affected by high concentrations of salt in agroecosystems, due to (i) natural biogenesis of agricultural soil located in arid and semiarid regions and/or (ii) application of high rate of synthetic fertilizers, irrigation, and backflow of seawater (Siddikee et al. 2010).

In different regions of the world, saline soils represent most of the arable and cultivable areas, so several strategies have been implemented to mitigate its effects and generate good yields. For example, tolerant plants to higher salinity concentrations by using genetic modification have been widely reported (Roy et al. 2014). As well as other techniques such as the selection of genotypes resistant to salt stress (first strategy) has shown that it may be another viable alternative and that it could be more accepted in certain legislations of countries where the cultivation of GMOs (second strategy) may be prohibited or highly restricted for cultivation (James 2015). A third strategy is the use of microorganisms that form beneficial interactions with plants, in particular, the plant growth-promoting bacteria (PGPB) (Lugtenberg and Kamilova 2009, Rojas-Solis et al. 2018). Thus, various bacterial genera from the rhizosphere, phyllosphere, or plant endosphere have been isolated and characterized by their ability to promote the growth of plants under salt stress conditions (Ghosh et al. 2003; Shrivastava and Kumar 2015). In this chapter we will focus on bacteria of the Bacilli group, mainly the *Bacillus* genus, within which there are several species that stand out for their multiple direct and indirect mechanisms of plant growth promotion, in addition to resistance to several types of environmental stress, fast-growing or duplication rate, and competent colonization, among others (Santoyo et al. 2012).

5.2 Salt Stress in Plants and Ethylene Biosynthesis

Ethylene is a hormone that is produced by the vast majority of plants and that occurs in various concentrations depending on the environmental conditions where the plants develop and grow (Glick 2014). Ethylene at optimal concentration (10 g L^{-1}) can induce seed germination and elongation of the roots and the formation of primordia in stems and roots and initiate the stages such as flowering. In fruits, it can induce ripening and degradation. Also, it may be part of the produced volatiles that are part of the compounds important in fruit aroma (Lynch and Brown 1997; Choudhary 2017). However, at a higher concentration (25 g L^{-1}), this hormone induces defoliation, inhibition of root elongation, leaf senescence and abscission, and chlorophyll destruction (Singh et al. 2015). Thus, it is determinant to control or regulate the ethylene production by roots for normal growth and development of the plants.

In plants, ethylene is synthesized in three steps: methionine is converted to S-adenosyl-methionine by S-AdoMet synthetase; then 1-aminocyclopropane-1-carboxylic acid (ACC) is synthesized from S-AdoMet by ACS (ACC synthase); and finally, ethylene is produced through the oxidation of ACC by ACO (ACC oxidase) (Lin et al. 2009).

Ethylene can be found in low concentrations in various plant tissues under stress-free conditions. The regulation of ethylene synthesis occurs at different steps of the biosynthetic pathway. In Arabidopsis, tobacco and cotton, expression of genes coding for ACSs was found to be increased under salt stress (Achard et al. 2006, Cao et al. 2006, and Peng et al. 2014a, b). Interestingly, in Arabidopsis it was also found that a moderate low salinity pretreatment alleviated salt stress induction of four ACSs (ACS2, ACS6, ACS7, and ACS8) (Shen et al. 2014). ACO is also regulated by salinity. In cotton, several ACOs were found to be upregulated after salt treatment (Peng et al. 2014b).

Ethylene synthesis is affected by several factors including temperature, light, nutrition, gravity, and the presence of various types of biological stresses, i.e., the plant growth under salt stress, which improves plant tolerance to high salinity (Peng et al. 2014a, b). Thus, ethylene and its precursor (ACC) are induced by salinity in plant species; in fact, ethylene is known as the "hormone of stress" (Arshad et al. 2008). Ethylene is not only produced in response to salt stress but as a generalized response caused by multiple types of stress. Besides, saline stress in plants causes a series of physiological responses, i.e., salinity in plants induces generation of reactive oxygen species (ROS), including superoxide anion (O_2^-), singlet oxygen ($^1O_2$), and hydrogen peroxide (H_2O_2), and causes cellular damage in the plant system (Arshad et al. 2008; Long et al. 2015; Peng et al. 2014a, b). In a recent work, it is proposed that salt stress can also block water absorbing by an osmotic stressful effect and a direct cell wall synthesis inhibition (Fig. 5.1). The previous stresses caused by the salt ends with a slow cell development and a shortage in root length (Long et al. 2015).

Thus, salinity causes a stress on the plant, which leads to an increase in the production of ethylene, causing the abscission of leaves, petals, and flowers. It can also cause yellowing of leaves, senescence of various organs, and premature death of the plant (Zahir et al. 2009). Ethylene synthesis pathways in plants have been reviewed in quite a lot of detail in various works and have been known in detail for years (Yang and Hoffman 1984, Gamalero and Glick 2012). Briefly, the enzyme ACC synthase converts the S-adenosylmethionine (SAM) to 1-aminocyclopropane-1-carboxylic acid (ACC) and 5′-methylthioadenosine (MTA). ACC is then converted to ethylene by the enzyme ACC oxidase. Indeed, it has been proposed that, while ethylene plays a positive role in the early stage of self-adjustment for survival under high-salinity stress, after self-adjustment has been achieved, excessive ethylene in plants will inhibit plant growth and development, which is disadvantageous for plants to survive under high-salinity stress (Tao et al. 2015).

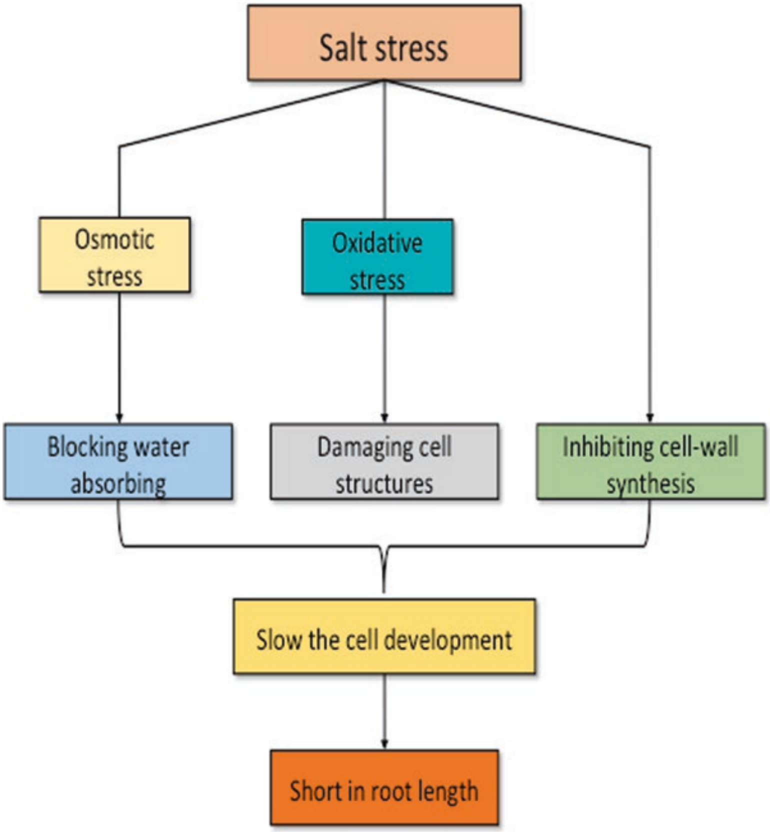

Fig. 5.1 Proposed model for root development inhibition under salt stress. See text for details. (Modified from Long et al. 2015)

5.3 Bacterial ACC Deaminase

The enzyme 1-aminocyclopropane-1-carboxylate deaminase (ACC deaminase) was first discovered and purified from an edaphic microorganism (*Pseudomonas* sp. ACP). This strain showed the ability to convert ACC to ammonia and α-ketobutyrate (Honma and Shimomura 1978). Thus, plants – under stress conditions, i.e., saline – respond by increasing the production of ethylene, causing various physiological changes that allow it to adapt and survive, such as tissue abscission and senescence. It is here where the bacterial enzyme ACC deaminase acts by degrading the plant ACC, the direct precursor of ethylene, generating α-ketobutyrate and ammonia, so the ethylene accumulation under stress conditions is avoided. Therefore, the bacterial enzyme ACC deaminase helps the plant to reduce the abiotic stress, promoting its growth and survival (Glick 2014). Glick and colleagues (1998) proposed the pioneering model on the action of the enzyme ACC deaminase as a relevant factor for growth promotion in plants. In general, the ACC deaminase-containing PGPB associated with plants act as a sink for ACC, generally causing an increase in the length of the roots and shoots, as well as a better resistance to the growth inhibition by the ethylene-inducing stresses.

In a more recent model (Fig. 5.2), Glick (2014) proposes that phytohormone indole-3-acetic acid (IAA), produced by the plant and the associated PGPB, plays an essential role during the promotion of plant growth. The roots of the plant exude various compounds to the rhizosphere, including sugars, organic acids, and amino acids, such as tryptophan. PGPB can assimilate tryptophan, which is an essential precursor of the IAA synthesis. Then, the PGPB that produce IAA (in addition to ACC deaminase) can induce the transcription of auxin response factors, promoting plant growth and transcription of the ACC synthase as well. In conclusion, PGPB that contain ACC deaminase and produce IAA can generate a cross talk in the plant between IAA and ACC deaminase. On the other hand, ACC deaminase lowers ethylene levels, while IAA stimulates plant growth (Duca et al. 2014; Nascimento et al. 2018).

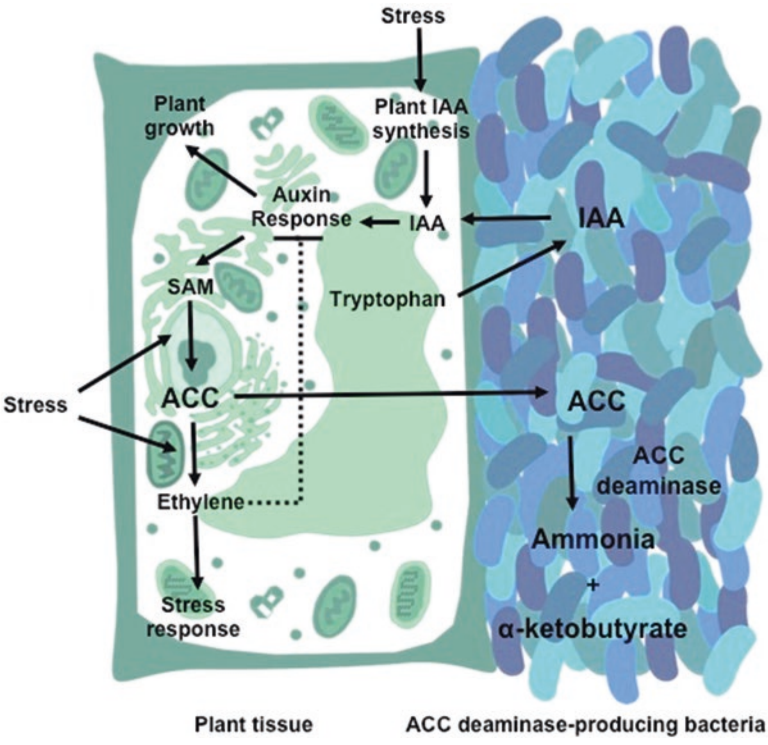

Fig. 5.2 Bacilli that both contains the enzyme 1-aminocyclopropane-1-carboxylate deaminase (ACC deaminase) and synthesize the phytohormone indole-3-acetic acid (IAA) may induce plant growth. The scheme is only showing the ACC deaminase enzyme and was modified from Glick (2014)

5.4 *Bacillus* Genus as Plant Growth-Promoting Bacteria

The *Bacillus* genus was first reported by Cohn in 1872 (Kokcha et al. 2012), who described it as heat-resistant, endospore-producing bacteria; at present, this genus includes over 336 species (Alcaraz et al. 2010). *Bacillus* is widely distributed worldwide (cultivable population from log 3 to log 6 per gram fresh weight of soil) (Vargas-Ayala et al. 2000) due to their ability to form endospores, a structure that provides them the ability to live in several habitats, both water and terrestrial ecosystems, and even in environments under extreme conditions (Tejera-Hernández et al. 2011). Regarding the agricultural sustainability, few researches have to be carried out to understand the diversity and dynamics of *Bacillus* in agroecosystems under stress conditions and how the crop with *Bacillus* interaction is modulated by extreme soil conditions.

Bacillus, among other PGPB, offers vital ecosystemic services, such as (i) social and ecological sustainability, (ii) adaptation and mitigation to climate change, (iii) biotechnological resource for humanity, (iv) cycling of water and nutrients, and (v) food security, mainly by nutrient cycling (van der Heijden et al. 2008), and improving the plant growth by avoiding the establishment of phytopathogenic agents (Compant et al. 2005), and the production of phytohormones, solubilization of nutrients, and activity of enzyme such as ACC deaminase (Hayat et al. 2010)

In the last decade, *Bacillus* strains have been reported to influence crop growth and yield under abiotic stress conditions, i.e., in a field experiment (Electric conductivity = 5.2 dS m^{-1}), Upadhyay and Singh (2015) reported a maximum root dry weight and shoot biomass after inoculation of wheat with *Bacillus aquimaris* SU44 and *B. aquimaris* SU8, after 60 and 90 days, respectively.

These traits make the Bacilli members excellent candidates for generating bio-inoculants, since, in addition to the aforementioned previous advantages, the spores can be stored for a long time, remaining viable until their inoculation in the field, which can survive even under adverse conditions such as saline stress (Villarreal-Delgado et al. 2018). Therefore, for several years Bacilli have been highlighted as effective bio-inoculants due to their consistent field results (Glick, and Skof 1986).

5.5 Presence of ACC Deaminase in Soil Microorganisms

The ACC deaminase activity has been reported in all three domains, i.e., Eukarya, Bacteria, and Archaea. This finding is corroborated by identifying the *acdS* gene in the genomes of soil microorganisms and endophytes, as well as the activity of the ACC deaminase enzyme, and is relatively frequent (Blaha et al. 2006; Nascimento et al. 2014). Plant fungi such as *Trichoderma asperellum* contain the ACC deaminase enzyme. *T. asperellum* has been reported as beneficial to plants, since it has phytopathogen biocontrol activity and plant growth-promoting traits (Viterbo et al. 2010). Bacterial groups such as *Rhizobiaceae* (*Rhizobium*, *Sinorhizobium*, and

Agrobacterium), *Phyllobacteriaceae* (*Phyllobacterium* and *Mesorhizobium*), and *Azospirillum* also contain the ACC deaminase enzyme (Nascimento et al. 2014). Other genera of PGPB bacteria that have been studied also exhibit deaminase ACC activities, including *Achromobacter*, *Burkholderia*, *Ralstonia*, *Pseudomonas*, and *Enterobacter* (Blaha et al. 2006; Duan et al. 2013; Wang et al. 2000; de los Santos-Villalobos et al. 2013).

In a recent work on the evolution and phylogeny of the *acdS* gene (ACC deaminase enzyme gene), the authors detect its presence in bacterial groups as diverse as *Actinobacteria*, *Deinococcus*/*Thermus*, *Alphaproteobacteria*, *Betaproteobacteria*, *Gammaproteobacteria*, and *Firmicutes*. Surprisingly, *acdS* genes were found in a wide range of plant and human pathogenic microorganisms, suggesting a different role in these organisms. The authors also reported the presence of Lrp-like regulatory proteins, such as AcdR, which is a common regulatory mechanism ACC deaminase expression in Proteobacteria (Nascimento et al. 2014).

5.6 Plant Growth Promotion by Bacilli Expressing ACC Deaminase

Bacilli are one of the most abundant bacterial groups in agricultural ecosystems; it is somehow expected to contain the *acdS* gene and, therefore, the ACC deaminase enzyme (Santoyo et al. 2012; Nascimento et al. 2014). The first report of the isolation and characterization of plant growth-promoting Bacilli with the ability to catabolize the ACC was carried out by Ghosh et al. (2003). In that work, the authors isolated plant growth-promoting bacteria from southeastern Wisconsin soils based on the unique ability of the isolates to use the ACC as the sole source of nitrogen. Thus, they isolated three Bacilli, including the species *Bacillus circulans* DUC1, *B. firmus* DUC2, and *B. globisporus* DUC3, which exhibited beneficial abilities by stimulating the root elongation in *Brassica campestris* (canola) seedlings under gnotobiotic conditions.

Other recent work has shown that several species of Bacilli show activities that promote plant growth associated with the ability of strains to use ACC. For example, Xu et al. (2014) carried out a screening in bacterial communities of *Bacillus* within the seeds of four commercial tomato varieties (*Lycopersicum esculentum* Mill.), by 16S rRNA gene PCR-RFLP (restriction fragment length polymorphism), in order to identify PGP traits under gnotobiotic experiments and greenhouse conditions. Thus, authors identified the strain *B. subtilis* HYT-12-1, which showed ACC deaminase activity, among other PGP mechanisms.

In another work, searching for plant growth-promoting endophytes associated with the medicinal plant *Lonicera japonica*, which grows in eastern China, several bacterial strains were identified, *Bacillus* and *Paenibacillus*. Such strains showed a promising ACC deaminase activity, as well as induction of root and shoots length and increment of chlorophyll of wheat (*Triticum aestivum* cv. “Zhoumai 18”). Also, some strains showed antagonism against the phytopathogens *Magnaporthe grisea*, *Fusarium oxysporum*, and *Alternaria alternata* (Zhao et al. 2015).

Two other endophytic strains of Bacilli, *B. subtilis* LK14 and LK15, were isolated from the medicinal plant *Moringa peregrina*, which grows in the arid regions of Arabia. The inoculation of one of the strains, LK14, significantly increased the shoot and root biomass and chlorophyll contents of tomato (*Solanum lycopersicum*) plants (compared to uninoculated plants). Interestingly, such strain exhibited a significant production of IAA, as well as ACC deaminase activity. Although the authors did not perform inoculation experiments under saline stress conditions, it can be concluded that using endophytic, Bacilli strains can be bio-prospective for plant growth promotion of crops in marginal lands (Khan et al. 2016).

5.7 Plant Growth Promotion by Bacilli Under Saline Stress

The previous works show a high potential to use plant growth-promoting Bacilli with ACC deaminase activity; however, there is no clear relationship between the ability to use ACC and the induction of growth in plants, in addition to the fact that the experiments were not carried out under stressful conditions, either salinity or other environmental stress, a situation where the ACC deaminase enzyme can have a potential to reduce ethylene levels in plants, facilitating survival and increasing plant growth. Therefore, the use of mutants in the *acdS* gene was necessary to confirm a relationship between ACC deaminase activity and the promotion of plant growth. Thus, Dr. Glick's group generated an *acdS* mutant in the bacterium *Pseudomonas* sp. UW4 (previously known as *Enterobacter cloacae* UW4), which showed a significant decrease in ACC deaminase activity and root elongation of canola plants. Thus, this work confirmed the importance of the ACC deaminase and validated the model where it is proposed that PGPB induce plant growth by lowering ethylene levels in plants, including ethylene inhibition of root elongation (Li et al. 2000).

In a recent work, Yaish et al. (2015) isolated and characterized several endophytic Bacilli (*Paenibacillus xylanexedens* PD-R6) of date palm (*Phoenix dactylifera* L.) with ACC deaminase activity, among other mechanisms such as the production of indole-3-acetic acid (IAA). Some strains were also able to chelate ferric iron (Fe^{3+}); solubilize phosphorus (PO43+), zinc (Zn2+), and potassium (K^{+}); and produce ammonia. The PD-R6 strain increased the root length of canola plants, either under normal growth conditions or salinity, but interestingly, it was possible to observe an increase in ACC activity and production of IAA in response to the increase in salt (NaCl) in the growth medium. The authors conclude that the isolated endophytic bacterium *Paenibacillus xylanexedens* PD-R6 can alter ethylene and IAA levels and also facilitate nutrient uptake in roots and therefore have the potential role to promote the growth of date palm trees growing under salinity stress.

The ability to produce IAA and the ACC deaminase activity displayed by Bacilli is a desirable feature in PGPB. Thus, Chinnaswamy et al. (2018) isolated to fast-growing, endophytic strain of *Bacillus megaterium* (NMp082) from root nodules of *Medicago polymorpha*. This species, apart from exhibiting to produce IAA and ACC deaminase activity, contained *nifH* and *nodD* genes with a 100% identity to those of *Ensifer meliloti*, which suggest an unusual event of lateral gene transfer. The authors also reported that *B. megaterium* NMp082 was not able to form effective nodules, but it induced nodule-like unorganized structures in alfalfa roots. Interestingly, *B. megaterium* NMp082 induced tolerance to salt stress in alfalfa and *Arabidopsis* plants and showed good traits to tolerate salt stress, water deficiency, and the presence of different heavy metals.

5.8 Plant Growth Promotion by Naturally Halotolerant Bacilli

Isolating strains that are naturally tolerant to high salt concentrations (halotolerant) is an excellent strategy to identify plant growth-promoting Bacilli strains, since usually these strains contain deaminase ACC activity. In countries such as Iran where 25% of arable land have high concentrations of salt, it is desirable to identify halotolerant strains as bioinoculating potentials that allow their survival in such stressful conditions and carry out effective plant growth-promoting actions. Recently, a halotolerant strain of *Bacillus mojavensis* K78 was identified in Iranian rhizospheric soils, which contains ACC deaminase activity and was able to increase dry root weight and shoots, chlorophyll content, and nutrient intake in low wheat plants conditions of salt stress. Additionally, strain K78 improved the water content of wheat grown under stress, improving the osmotic balance of plant cells (Pourbabaee et al. 2016).

Other halotolerant strains of *Bacillus* with ACC deaminase activity have been reported. For example, the species *B. aryabhattai* strain RS341 showed more than 40% increase in root elongation and dry weight in canola seedlings, when compared with uninoculated salt-stressed plants (Siddikee et al. 2010). More recently the same group reported that the inoculation of ACC deaminase-producing halotolerant *B. aryabhattai* RS341 at 120 mM of NaCl significantly increased the seed germination and decreased seed ACC content. Importantly, the ethylene emission of salt stress exposed canola seedlings was reduced with the inoculation of strain *B. aryabhattai* RS34, compared to uninoculated salt stress control. The authors concluded that amelioration of salt stress inhibitory effect on the canola seed was attributed to the modulation in ethylene emission (and induction of hydrolytic enzymes) by bioinoculation of ACC deaminase-producing halotolerant strain RS341 (Siddikee et al. 2015). Table 5.1 shows relevant works of ACC deaminase-producing Bacilli species that promote plant growth under salt stress conditions.

Table 5.1 Bacilli species producing ACC deaminase and containing other direct and indirect mechanisms to induce plant growth

Bacilli species and strain	Plant host/ endophyte or rhizospheric origin	Plant growth-promoting effect	References
Bacillus megaterium NMp082	*Medicago polymorpha*/ Endophyte	Promote plant growth in *Medicago* spp.	Chinnaswamy et al. (2018)
		Induce tolerance to salt stress in alfalfa and Arabidopsis plants	
B. circulans DUC1	Alfalfa, soybean, tomato, corn/	Promote plant growth in canola seedlings	Ghosh et al. (2003)
Bacillus firmus DUC2	Rhizospheric		
B. globisporus DUC3		Low ethylene levels	
		Root elongation is enhanced	
B. aryabhattai RS341	Halophytic plants/ Rhizospheric	Increase root elongation and dry weight in salt-stressed canola seedlings	Siddikee et al. (2010)
B. aryabhattai	Halophytic plants/ Rhizospheric	Alleviate salt stress effect in canola seed germination	Siddikee et al. (2015)
RS341			
B. subtilis LK14	*Moringa peregrina*/ Endophyte	Improve the growth of tomato plants	Khan et al. (2016)
B. subtilis LK15		Produce IAA	
		Phosphate solubilization	
		ACC deaminase activity	
B. mojavensis K78	Wheat plants/ Rhizospheric	Facilitate plant growth promotion in the presence of inhibitory levels of salt in wheat plants	Pourbabaee et al. (2016)
		ACC deaminase activity	
B. subtilis HYT-12-1	Tomato seeds/ Endophyte	Promote plant growth in tomato plants	Xu et al. (2014)
		ACC deaminase activity	
		Fix Nitrogen	
B. megaterium QM B1551	Date palm (*Phoenix dactylifera* L.)/ Endophyte	Some strains have ACC deaminase activity and produce IAA and ammonia (except *Bacillus megaterium* QM B1551)	Yaish et al. (2015)
B. endophyticus 2DT			
B. oleronius ATCC			
B. thuringiensis Bt407			
B. anthracis Ames			
B. atrophaeus 170	*Lonicera japonica*/ Endophyte	Promote plant growth in wheat plants. Strain 124 shows capacity for siderophore production and phosphate solubilization	Zhao et al. (2015)
B. megaterium 124			
B. subtilis 132			
B. subtilis 135			

5.9 Conclusions and Perspectives

The Bacilli have great potential versus other groups of PGPB, for example, the capacity to sporulate, the high tolerance to saline stress, fast-growing rate and elevated competence to colonize niches in the rhizosphere are common traits in newly isolates around the world, as well as its wide distribution in different latitudes, noticing the good capacities to promote plant growth of plants through ACC deaminase activity, without ruling out other mechanisms that allow an additional benefit. For example, Bacilli can enhance the efficiency of water use and nutrient uptake, as well as maintaining K^+/Na^+ ratio in plant cells (Nadeem et al. 2007).

It is noteworthy that there is a lack of knowledge regarding the level of participation of the ACC deaminase with respect to other mechanisms of stimulation of growth and development in plants; this is, in part, due to the lack of mutant strains and double mutants (i.e., ACC deaminase gene plus other genes that encode mechanisms such as production of siderophores, solubilization of nutrients, and production of osmoprotective compounds) that have delayed their analysis in the plant-bacteria interaction. Therefore, it is essential that this area of genetic analysis be developed further to allow the evaluation of the cross talk between functions and bacterial mechanisms of PGP. Finally, we propose that more work needs to be done on the interaction between various species of Bacilli and other PGPB, since it has been observed, in a few recent works, the additive and/or synergistic activity of Bacillus species with other beneficial bacterial species or fungi (Armada et al. 2016; Kumar et al. 2016). Finally, whether a bioinoculant containing different PGPB is developed, the presence of one or more species of the Bacilli group is essential, since such species have enormous potential to benefit plant health, particularly, those agroecosystems with problems of salinity.

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