Review Article

ERA'S JOURNAL OF MEDICAL RESEARCH

VOL.9 NO.1

DOI:10.24041/ejmr2022.09

ROLE OF ACC DEAMINASE PRODUCING PLANT GROWTH PROMOTING RHIZOBACTERIA IN AMELIORATING THE SALINITY STRESS CONDITIONS: A REVIEW

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Received on : 07-06-2022
Accepted on : 21-06-2022

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ABSTRACT

Salinity in agricultural soil is a severe problem that affects the growth and production in numerous crops all over the world. The country's salt–affected land is estimated to be 6.74 million hectares. According to estimates, approximately 10% more land is becoming salinized each year, and by 2050, nearly half of all arable land will be contaminated by salt. Plants may have bacterial companions that shield them from the negative consequences of salt stress (SS). Plant growth–promoting bacteria (PGPR) can minimize the usage of agrochemicals while also improving plant production, nutrition, and biotic–abiotic stress tolerance. The enzyme 1– aminocyclopropane–1–carboxylic acid deaminase (ACCD) is found in certain bacteria and works by degrading ACC (ethylene precursor in higher plants) into α–ketobutyrate and ammonia (NH_3), thereby reducing the ACC levels, thus, inhibits excessive biosynthesis of ethylene under numerous stress circumstances. This is one of the most effective methods for inducing plant tolerance to SS. The current review highlighted the recent works of ACCD under SS environment. Further, the relevance of reducing the negative effect of ROS and increasing plant development under SS were also discussed. We propose a path for the community to employ beneficial microorganisms to boost agricultural yield and achieve sustainable development by highlighting plant–microbe interactions in this review.

KEYWORDS: Plant stress, salinity stress, PGPR, Pisum sativum, ACC deaminase

INTRODUCTION

Agriculture has been the biggest financial basis since the dawn of human civilization. Approximately 7.4 billion (bln) persons inhabit the earth and occupy 6.38bln hectares of the earth's surface, of which 1.3 bln people depend directly on agriculture. Food and Agriculture Organization of the United Nations (FAO) balance sheet 2004 estimates that 99.7% of global food for the earth's population comes from the terrestrial environment. According to the FAO estimates, 38.5% of the global land area is sheltered by agricultural land, and despite the fact that 28.4% of the land is fertile, only 3.13% is completely used for crop production. The situation in addition has further deteriorated as 20–25% of the land is degraded annually worldwide (1). It has been estimated that the current salt–affected area would almost triple from 6.73 million to 20 million hectares by 2050 in the country (2). In India, 60.6% of the land is utilized for agricultural purposes and nearly half of its population grew different forms of vegetables, cereals, and pulses (3).

Agriculture is one of the human activities that contributes the most to the increase in chemical pollutants due to the overuse of artificial pesticides and fertilisers. This poses additional risks to persons or mankind, as well as harming the environment. Fertilizers have become essential components in modern agriculture because they feed plants with essential minerals such as nitrogen (N), phosphorus (P), and potassium (K) . The overuse of these chemical fertilizers has a deadly impact on ecologies such as by reducing crop productivity and soil fertility (4). Now, the situation is quite alarming, therefore, studies are needed to find a low–cost, eco–friendly, and easy–to–use solution to solve the problem of fertilizer toxicity.

Plant growth-promoting rhizobacteria (PGPR) as rhizospheric microorganisms have become an important part of sustainable agriculture, enhancing soil fertility (5,6). The rhizosphere is the zone surrounding plant roots in which the plant and numerous soil microorganisms have multilayered relationships. Hiltner created the word "rhizosphere" in 1904 to describe an area with massive microbiological activity. The bacterial diversity in the rhizosphere is generally known to be substantially higher than in rootless soil. This is due to the presence of nutrients secreted by the plant roots, such as amino acids, sugars, organic acids, and other small molecules. (7,8).

The plant microbiome aids crops in obtaining nutrients, combating diseases, and tolerating biotic and abiotic stressors (9). Numerous rhizospheric bacteria can act as biofertilizers and also increases the plant tolerance toward SS (10). In unstressed soils, rhizospheric bacteria can reach 108 or 109 microbial cells per gramme of soil, however in stressed soils, the microbial population can drop to 104 cells per gramme of soil. (11). Bacteria that colonize the roots of plants (rhizosphere) and increase plant development through diverse processes are referred to as "plant growth–promoting bacteria." Nodule Promoting Rhizobacteria (NPR) or Plant Health Promoting Rhizobacteria (PHPR) are bacteria that are connected to the rhizosphere, which is an essential ecological habitat for plant–microbe interactions in soil (12). Many PGPR are linked to a variety of microorganisms as well as arbuscular mycorrhizal fungus (AMF), resulting in a multilateral interaction that boosts plant development and productivity. PGPR can be classified as freeliving bacteria (those that live outside of plant cells and trade metabolites) or symbiotic bacteria (those that reside inside plants and exchange metabolites) (13). These PGPR can be divided into two groups based on where they live: (1) extracellular (ePGPR), which live in the rhizosphere, on the rhizoplane, or in the spaces between cells of the root cortex, and (2) intracellular or symbiotic bacteria (iPGPR), which live inside the nodular structures of the rhizome.

Many PGPRs have two types of functioning mechanisms: direct and indirect. Root growth stimulation, biofertilization, rhizoremediation, nitrogen fixation, phosphate solubilization, and ACC (1aminocyclopropane1carboxylic acid) deaminase activity are some of the direct methods. PGPRs are not only associated to the root in terms of their good impacts for plant growth, but they also contain a number of antimicrobial properties. (14, 15). The principal mechanisms of plant growth promotion includes production of phytohormones, siderophore production, mobilization and solubilization of phosphate, antibiosis, such as antibiotics production, inhibition of biosynthesis of ethylene hormone, and induced systemic resistance towards pathogenic attack in crops (16). The successful utilization of PGPR is mainly dependent upon its survivability in soil, its interaction with indigenous microflora in soil, its compatibility with various crops, and several ecological factors (17). The use of genetically modified PGPR strains for practical purposes is now being considered, due to the development of genetic engineering (18). Many PGPR have the potential to limit pathogenic bacteria' negative impacts on plants by creating a variety of growth inhibitors such as siderophores, antibiotics, bacteriocins, and lytic enzymes, as well as improving plant natural resistance to pathogens. PGPR's antagonistic activity is controlled by a variety of processes, including siderophores, parasitism, competition, and antibiotic synthesis. (19). Some rhizobia strains can produce biomolecules, and siderophores, that act as specific iron–chelating agents, often in–accessible to living beings and are essential for accomplishing dynamic functions including Biological nitrogen fixation (BNF), respiration, photosynthesis, and DNA biosynthesis (20). Thus, we can reduce the dependency on chemical fertilizers and their application in the agriculture sector, as these practices have unfavorable effects on ecology (21).

PISUM SATIVUM AND ITS NUTRITIOUS VALUE

In the Fabaceae family, Pea (*Pisum sativum* L.) belongs to the Faboideae subfamily and Fabeae tribe. It is one of the essential cool–season vegetable crops generally grown all over the world. Planting pea seeds is allowed once the temperature reaches 10°C, while the optimal plant temperatures range from 13 to 18 °C, and crops require pH levels between 6.5 and 7.5 to grow successfully. It is an edible and nutritious crop that contains a higher proportion of carbohydrates, and vitamins, along with digestible proteins and mineral matter (22,23). Based on *FAO statistics, 2014*, India occupied 4th position in terms of area (10.53%) and 5th position in terms of production (6.96%), with its quantity increasing every year (Fig. 1). About 60% of India's field pea production is in Uttar Pradesh (U.P.) followed by Madhya Pradesh (M.P.).

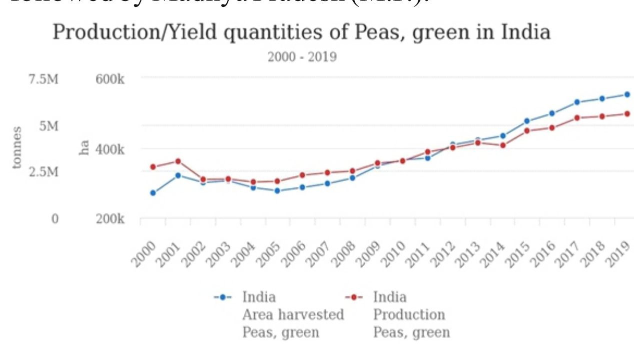

Fig. 1: Pea Production / Yield (Tonnes) in India

Pea has a diversification of nutritious values and is an adequate source of antioxidants enzymes and essential nutrients (**Table 1 and Table 2**).

S.No.	Essential Nutrients	Concentration
1.	Carbohydrate	62.1%
2.	Protein	22.5%
3.	Fat	1.8%
4.	Moisture	11%
5.	Calcium	64mg/100g
6.	Iron	4.8mg/100g
7.	Calorie	81/100g

Table 1: Nutritious Value in Pisum Sativum

Source: Ministry of Agriculture & Farmers Welfare, Directorate of Pulse Development, Bhopal (M.P)

(Source: USDA National Nutrient database)		
Principle	**Nutrient Value**	**Percentage of RDA**
Energy	81 Kcal	4%
Carbohydrates	14.45 g	11%
Protein	5.42 g	10%
Total Fat	0.40 g	2%
Cholesterol	0 mg	0%
Dietary Fiber	5.1 g	13%
Vitamins		
Folates	65 µg	16%
Niacin	2.090 mg	13%
Pantothenic acid	0.104 mg	2%
Pyridoxine	0.169 mg	13%
Riboflavin	0.132 mg	10%
Thiamin	0.266 mg	22%
Vitamin A	765 IU	25.5%
Vitamin C	40 mg	67%
Vitamin E	0.13 mg	1%
Vitamin K	24.8 µg	21%
Electrolytes		
Sodium	5 mg	<1%
Potassium	244 mg	5%
Minerals		
Calcium	25 mg	2.5%
Copper	0.176 mg	20%
Iron	1.47 mg	18%
Magnesium	33 mg	8%
Manganese	0.410 mg	18%
Selenium	1.8 µg	3%
Zinc	1.24 mg	11%
Phyto-nutrients		
Carotene-ß	449 µg	
Crypto-xanthin-ß	0 µg	
Lutein-zeaxanthin	2477 µg	

Cont. Table 2: Analysis of Nutrition Value in Green Peas (Pisum Sativum), Fresh, Raw, Per 100 gram

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Source: https://www.nutrition-and-you.com/green-peas.html

ABIOTIC STRESS

Abiotic stresses include soil salinity, low and high temperature, light, drought, flood, wind, et al. (24). Abiotic stresses such as SS have the potential to greatly affect crop productivity as well as crop quality (25–27). In addition, abiotic stress also reduces the Cytokinin content or signaling thereby reducing the shoot growth that often increases resistance towards abiotic stress (28).

AGRICULTURAL SALINE SOILS AND THEIR TOLERANCE

Saline soils have high electrical conductivity (ECe) because of the high concentrations of soluble salts, such as sodium (Na), calcium (Ca), and magnesium chloride ($MgCl_2$). Sodium chloride (NaCl) provides a high amount of soluble salts and causes salinity problems in soils (29). It has been evaluated that salinity affects around 800 or 1000 million hectares (mha) of agricultural soil worldwide, which can be classified as alkaline–saline, acid–saline, and saline soils (30). India is experiencing a huge salinity problem in many states, Gujarat leading the way followed by U.P. and Maharashtra (**Figure 2**). Over–accumulation of salt in topsoil has a deleterious impact on crop productivity. As a result, salt–tolerant crops and their management might be a key method for boosting the agricultural economy (30).

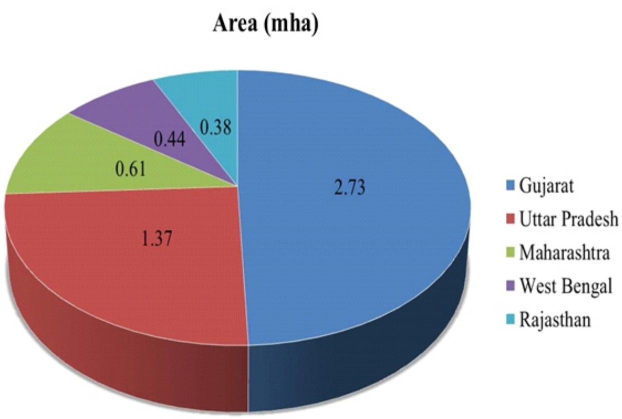

Fig. 2: Area Wise Salinity Affected States in India

SALINITY STRESS: A MAJOR CHALLENGE FORAGRICULTURE

Salinity in agriculture refers to salt levels that are higher than the plant's requirements (31). Electrical conductivity (ECe) is the unit of measurement (25). Salinity soil is defined by conductivity more than or equal to 4dS m1 according to USDA (United States Department of Agriculture) Salinity Laboratory Staff (1954). (32). Numerous cations such as Na+ (sodium), Ca2+ (calcium), K+ (potassium) and anions Cl (chloride), NO3 (nitrate) create soil salinity under various situations. Salinity reduces microbial activity and generates harmful consequences (due to the presence of ions) as well as osmotic stress, which causes plant development to slow. It reduces agricultural soil's water potential and makes it harder for crops to absorb nutrients and water from the soil, resulting in osmosis stress. Salinity stress affects all areas of growth, including seed germination, agricultural production, nutrient and water intake, as well as disrupting ecological and physicochemical balance. (33).

Salt stress affects crops in various ways, including deteriorating growth, photosynthetic capacity, nitrogen content, and metabolic processes, as well as protein and lipid metabolism (34). It has been reported that SS has drastically affected the yield and growth of several crops (26,27,35). Generally, the effects of salt–stress can be classified as (1) unavailability of water that causes drought–like conditions; (2) high salt content (i.e., Na^+ and Cl^-) in plants, resulting in disruption of biological and physiological processes; and (3) high salt content adversely affecting the soil nutrient availability. Stunted growth is a primary symptom of SS. Other effects of SS are a cessation of leaf expansion and a decline in the fresh and dry weights of roots, leaves, and stems (36). Salt stress largely affects shoot growth, in comparison to root growth, affecting both the reproductive and vegetative phases of plants (26). Due to high salt concentration and less water content, SS creates ionic and osmotic stress respectively (26). Soil salinity reduces the water and mineral uptake through roots from the soil within the cell that are toxic to plant cells for their growth. This results in reduced plant growth (36) and ion accumulation (mainly Na^+) mainly in leaf tissues leading to necrosis. “Necrosis is described as yellowing or darkening of plant tissue caused by the death of tissue. Due to a decrease in photosynthetic pigments, chlorosis symptoms appear on plants leaves. Therefore, roots with high solute concentrations have difficulty absorbing water and reduce the root conductivity. These effects further lead to decreased photosynthetic rate and plant growth. The chlorophylls and carotenoid content in leaves were also declined under SS. Salinity stress affects various physiological processes like reduction in permeability (due to dehydration), senescence, cessation of carbon assimilation in leaves, closure of stomata (that affect chloroplast activity), altered enzymatic activity, ionic leakage into the cytosol leading to inactivation of electron transport thereby affecting photosynthesis (37,38). Sodium ions (Na^+) interfere with root transporters and hinder root growth, preventing nutrient uptake by a plant (31). As SS leads to water deficit, it produces reactive oxygen species (ROS) that can cause secondary DNA damage, including DNA–protein crosslinks, loss of bases, and double–stranded DNA breaks (**Figure 3**), which leads to cell death and membrane dysfunction (26,27,39,40).

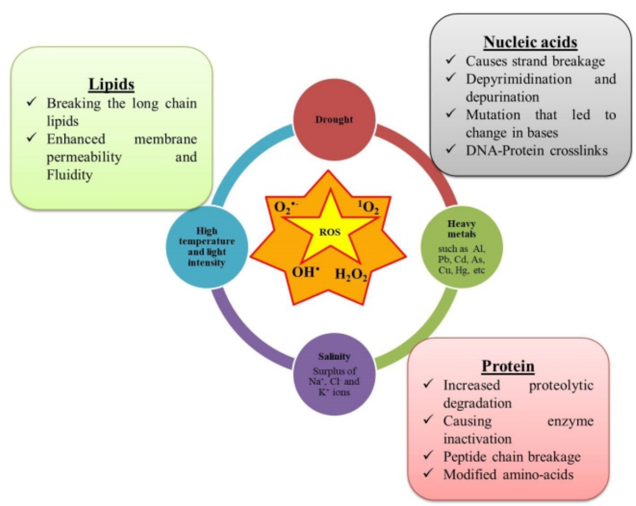

Fig. 3: Factors that led to ROS Generation, Damages the Targets Thereby Affecting the Plasma Membrane and Cellular Components.

Therefore, to cope up with these ROS and their adverse effect, plants respond with several non–enzymatic and enzymatic scavengers that alleviate the ROS–induced damage to a plant cell (26,27,41). Transgenic *Camelina sativa* lines harboring the bacterial acdS gene have been shown to have enhanced NaCl tolerance by controlling gene expression involved in the production of ROS, minimizing cellular damage (41). Moreover, plants treated with ACCD (1–aminocyclopropane–1–carboxylate deaminase) producing PGPB have been reported to increase the salinity tolerance, by positively regulating the abscisic acid and ethylene signaling. Substantially, an increase in salinity causes plant stress that up–regulated the biosynthetic pathway of "stress hormone" ethylene (42). As ethylene levels grow, a series of processes occur, including leaf yellowing, senescence of various plant parts, abscission of leaves, flowers, and petals, and even death (43). Furthermore, ethylene has been shown to have a crucial role in plant microbe interactions. (26, 44). A variety of salt–tolerant (ST) microbes are involved in promoting plant growth under stress conditions. Considerably, it has been well documented, that inoculation with PGPM (Plant Growth Promoting Microbes) mitigates the damaging effect of NaCl on various crops through several direct and indirect mechanisms. Lettuce seed inoculated with *Azospirillum* bacterium showed better vegetative growth and germination compared to control under saline conditions (45). In another study, inoculation of plants with PGPB *Bacillus* and *Pseudomonas sp.* reduces the adverse effect of salinity on salt–sensitive *Pisum sativum* (26).

Rhizobacteria that produce ACC deaminase (ACCD) can convert ACC to ammonia (NH3) and alphaketobutyrate (kb), reducing ethylene levels. PGPM reduces SS by collecting osmolytes in their cytoplasm, preventing osmotic stress and preserving plant development and cell turgor. Microbial EPS bind to cations in reaction to salinity, rendering them inaccessible to plants (46). Coinoculation of Pseudomonas and Rhizobium with Zea mays resulted in increased proline accumulation and decreased electrolyte leakage. (47). The stress tolerance in the maize crops is due to a reduction in osmotic potential, electrolyte leakage, selective uptake of K^+ ions and enhanced production of proline. *Bacillus pumilus* and *Pseudomonas pseudoalcaligenes* inoculated rice crops enhance salinity tolerance and produce glycine betaine in higher concentrations (48). *Pseudomonas* and *Acetobacter* species produce ACCD and IAA during SS on barley and oats, thereby promoting plant growth (49). Nautiyal et al. (2013) found that ST bacteria *Bacillus amyloliquefaciens* NBRISN13 increased salt tolerance and rice plant growth by up–regulating and repressing 14 genes. In tomato plants, the tricarboxylic acid (TCA) cycle contributes to salinity tolerance (51).

ETHYLENE IN SALINITY STRESS

Ethylene is a gaseous hormone that regulates and manages plant growth and development, as well as controlling or adjusting plant responses to external challenges and participating in systematic growth (52). When the ethylene content in plant tissues was examined, two peaks of ethylene were discovered. Plants typically experience a smaller peak at an early stage of stress exposure, serving as a signal to activate protective responses triggered by the stress. A second peak, however, may appear several days after stress application and is much larger than the first peak (**Figure 4**). Almost every part of the plant suffers from chlorosis, senescence, abscission, and cell damage when it is exposed to this level of stress ethylene (53). The ACC in plant tissues is also very low at the start of stress conditions since ACC is a precursor to ethylene synthesis. An enzyme called ACC oxidase (ACO) converts a great deal of ACC into ethylene in this process. ACO is responsible for autocatalyzing its synthesis and for switching on the expression of ACC synthase (ACS) under stress (54). Following the consumption of ACC, ethylene production lags until ACS produces more ACC **(Figure 4)**. Stress enhances ACS's enzymatic action (55) and its genes are affected by environmental and developmental cues (56). Furthermore, some enzymes can degrade (1aminocyclopropane1carboxylic acid) ACC (ethylene precursor) and SAM (Sadenosyllmethionine). Some ethylene inhibitors have been shown to reduce ethylene levels without altering plant physiology (57). and that many plants have developed SS tolerance as a result of reduced ethylene levels (58).

1–AMINOCYCLOPROPANE–1–CARBOXYLIC ACID (ACC) DEAMINASE

An enzyme known as ACCD uses vitamin B6 and is classified under the tryptophan synthase family. Under stress, ACCD metabolizes ACC to form α–kb and NH_3, which controls ethylene production (26). For example, *Rhizobia* can metabolize ACC to make α–kb and NH_3 which is used as a sole source of C (carbon) and N (nitrogen). The ethylene growth regulator stimulates the growth of plants by initiating seeds germination, root development, fruit ripening, and inhibiting root extension (59) as well as providing relief from abiotic and biotic stress (59). During adverse conditions, endogenous levels of ethylene are increased to a deleterious level **(Figure 4)**and negatively affect root growth. ACCD producing PGPR could degrade ACC (an ethylene precursor) without altering the natural function of ethylene on plant growth (60). In plants, ethylene is involved in several metabolic processes at a minimum quantity (61). Rhizobacterial strains having ACCD activity enhance phytoremediation efficiency and many other plant growth parameters (62).

Several *acdS*$^+$ (ACCD positive) bacterial strains, like *Rhizobium japonicum, R. leguminosarum bv. viciae, Bradyrhizobium japonicum, Mesorhizobium loti, Bacillus pumilus, B. marisflavi, B. cereus* and *Sinorhizobium meliloti* are known to produce ACCD enzyme (63,64). Glick (2014) reported that bacteria producing IAA produce high levels of ACCD thereby inhibiting the 2nd peak of ethylene. It has been observed that a gene encoding ACCD (*acdS*) in *Mesorhizobium sp.* is controlled by nif gene promoter, which controls the nitrogen fixation gene (63).

dealing with abiotic stresses since the 1950s (64–66). The abiotic stress of plants can be alleviated by microorganisms that have intrinsic metabolic and genetic abilities (67). Several genera such as *Azospirillum* (68), *Azotobacter* (69), *Pseudomonas* (70,71), *Rhizobium* (71), *Bacillus* (26,71), *Trichoderma* (72), and *cyanobacteria* (73) appear to play an important role in promoting plant growth and mitigating severe abiotic stress. Moreover, studies have shown that *Bacillus* and *Pseudomonas* that produces ACCD can alleviate SS (74). Microorganisms move toward root exudates through chemotactic movement to colonize the roots. Based on their inherent capabilities, modes of interaction, and competitive survival conditions, In the rhizosphere microenvironment around plant roots, PGPR may operate as phytostimulators, biocontrol agents, and biofertilizers. Plant-microbe interactions thus play a

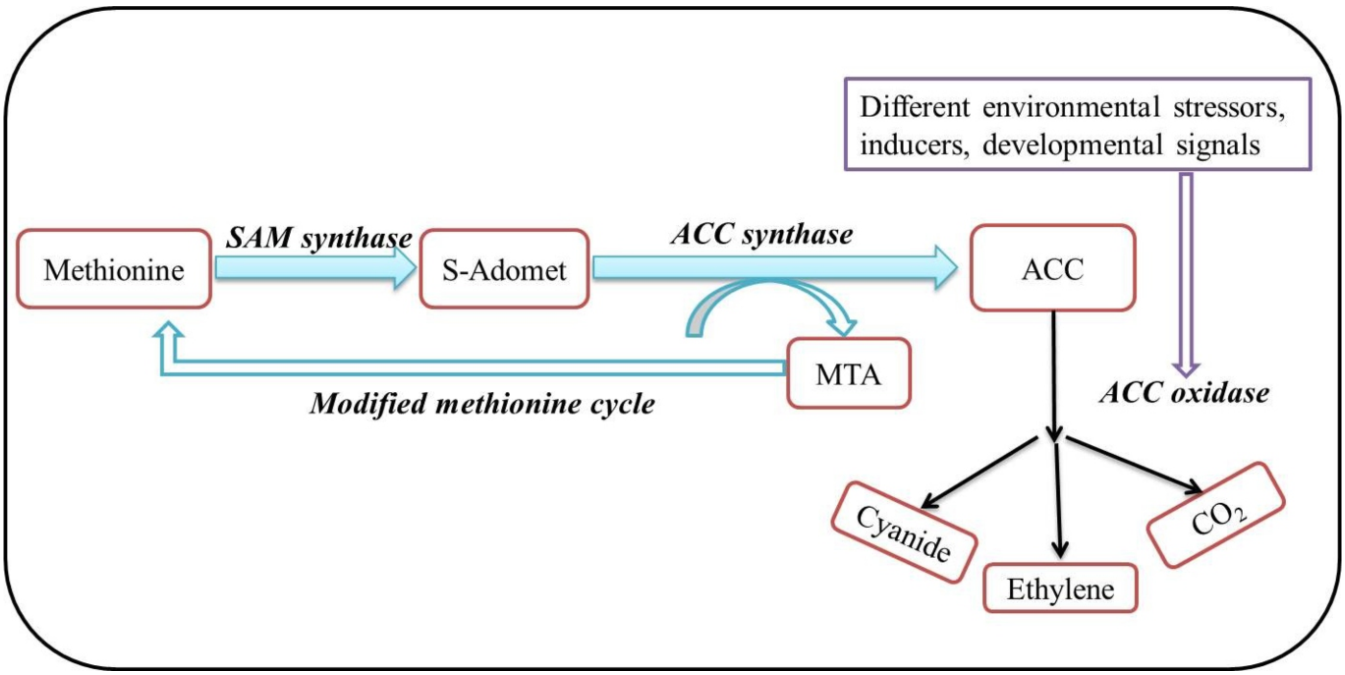

Fig. 4: Yang Methionine Pathway for Ethylene Biosynthesis. S–adenosyl Methionine (SAM) Synthase uses Methionine as a Precursor for SAM, while ACC Synthase Converts SAM to ACC.

MITIGATING ABIOTIC STRESSES THROUGH MICROBIAL MECHANISMS

Both crop plants and microbes need to interact with each other in order to adapt and survive in abiotic environments. Microbes induce abiotic stress responses through induced systemic tolerance (IST) and enhanced tolerance to SS*Azospirillum* strains that can tolerate water stress and SS (SS), improve plant growth, grain weight, and other performance characteristics of wheat crops (33,63). It has been well documented that microorganisms can aid plants in

diverse role. Plants can harvest and improve their growth by fixing, mobilising, and producing vitamins, hormones, and organic phytostimulants in their soil. On the one hand, microbes induce systemic or local stress alleviation response mechanisms in plants to facilitate plant survival under environmental stress conditions, while on the other hand, plants can harvest and improve their growth by fixing, mobilising, and producing vitamins, hormones, and organic phytostimulants in their soil. Microbes or their communities with such diversified actions are viable, powerful, and vital for crop plant abiotic stress mitigation.. Several soil–dwelling microbes belonging to genera *Azospirillum, Variovorax, Achromobacter, Azotobacter, Enterobacter, Klebsiella Aeromonas, Pseudomonas* and *Bacillus* can enhance the plant growth in a variety of environmentally unfavorable conditions (71,75–78).

PLANT GROWTH–PROMOTING RHIZOBACTERIA (PGPR)

Naturally occurring soil bacteria called plant growth–promoting rhizobacteria that inhabit the rhizospheric zone and help the plants to grow by enhancing productivity and resistance under normal and stressed conditions (79). Plants' tolerance to drought and salinity is largely thought to be mediated through PGPR (27,80). To reduce the impact of salinity and limited water, plants need to decrease their cell water potential to continue taking up water. Aquaporins (AQPs) appear to play an important role here, but Chaumont et al. (2005) conclude that microbiome–host interactions have specific responses that require further analysis (81). As a result, inoculation with *Bacillus megaterium* exhibited higher root hydraulic conductivity in salinity conditions (82). The direct mechanisms include the production of various phytohormones (like auxin, gibberellins, ethylene and cytokinin), siderophore production, biological nitrogen fixation (BNF), and nutrient mobilization (12). These mechanisms resulted in improving the surface area, root number, root length, and nutrient uptake (83). The rhizospheric bacteria like *Bacillus subtilis* isolated from saline soil displayed PGPR traits, like IAA production, HCN and NH_3 production, solubilization of phosphate, and also SS tolerance (84). Additionally, biofilm–forming PGPR is also very effective in alleviating the toxic effects of salinity (84). Moreover, some bacteria also possess sigma factors that can change the genetic expression during adverse conditions to overcome adverse effects (**Table 3**) (85). Thus, PGPR has shown itself to be a viable alternative to pesticides and inorganic fertilizers.

SOS1–Plasma membrane Na^+/H^+ transporter; NHX1–tonoplast Na^+/H^+ antiporter; HKT1– Sodium transporter; EREBP– Ethylene responsive element binding protein; EPS– Epoxypolysaccharide; ERK1–extracellular signal–regulated kinase1; NADP–ME2– NADP–malic enzyme 2.

PLANT GROWTH–PROMOTING BACTERIA CONTAINING ACC DEAMINASE

It is reported that ACCD activity is comparatively typical within the plant microbiome particularly in stressful ecosystems (11) demonstrating the importance of this activity for communication between plants–microbe. The *acdS* gene can be screened to determine whether ACCD is active in PGPB. The acdS gene's activity has been found to be common in bacteria, soil microorganisms, and endophytes, according to population assessments employing in silico or in vivo approaches (94–96). A phylogenetic analysis of the *acdS* gene confirmed that this enzyme was prevalent in various bacterial groups such as Deinococcus/Thermus, Actinobacteria, α, β, and γ Proteobacteria, and Firmicutes (95). It is interesting to note that some of the *acdS* genes are also found in human and plant pathogens; additionally, AcdR (Lrp–like regulatory proteins), which regulate *acdS* gene expression in proteobacteria, were also discovered (95). However, research has shown (97) that ACCD–containing bacteria *Arthrobacter protophormiae*, interacts with another beneficial microbe, promoting mycorrhizal colonization and rhizobial nodulation, leading to salt tolerance in *Pisum sativum* plants (97–99).

ACC deaminase was first discovered in rhizobia in 2003 (100). The ACCD can also significantly enhance and improve *Rhizobium* nodulation capacities and nitrogen fixation in pea plants by 40% (100) although the ACCD activity of rhizobia is extremely low compared to saprophytic bacteria. Earlier, the enzyme was only discovered in free–living bacteria, fungi, and yeasts. The ACCD activities of numerous PGPB have been observed, including *Achromobacter*,

PGPR	Crop plants	Beneficial effect/Mode of action	Reference
B. amyloliquefaciens SN13	*Oryza sativa*	Up–regulation of *SOS1, NADP–Me2, SERK1,* and *EREBP*	(50)
B. amyloliquefaciens SQR9	*Zea mays*	Up–regulation of *RBCL, HKT1, RBCS, NHX1, NHX2,* and *NHX3*	(86)
Bacillus megaterium	*Zea mays*	Increased root expression of two ZmPIP isoforms due to high hydraulic conductance	(82)

Cont. Table 3: Interactions between PGPR and various plants under abiotic stress

PGPR	Crop plants	Beneficial effect/Mode of action	Reference
Pseudomonas putida UW4 (ACCD)	*Solanum lycopersicum*	Elevated the expression of Toc GTPase and increased shoot growth	(87)
Bacillus subtilis GB03	*Arabidopsis thaliana*	Tissue–specific regulation of sodium transporter *HKT1*	(88)
Burkholderia, Arthrobacter and *Bacillus* sp.	*Vitis vinifera, Capsicum Annuum*	Elevated proline accumulation	(89)
Azospirillum brasilense and *Pantoea dispersa* (Co–inoculation)	*Capsicum annuum*	High photosynthesis and stomatal conductance	(90)
Bacillus subtilis	*Arabidopsis thaliana*	Root transcriptional expression of a highaffinity K+ transporter (AtHKT1) was reduced, and root Na+ import was reduced.	(91)
Pseudomonas putida strain GAP–P45	*Helianthus annuus*	EPS production	(92)
Rhizobium leguminosarum	*Brassica juncea*	Chelating compounds for metals	(93)

Cont. Table 3: Interactions between PGPR and various plants under abiotic stress

Arthrobacter, *Bacillus, Pseudomonas, Burkholderia*, *Brevibacterium*, *Citrobacter, Leclercia*, *Enterobacter*, *Micrococcus*, *Parastrephia*, *Ochrobactrum, Serratia,* and *Ralstonia* (26,33,101–104).

Several manuscripts have indicated that ACCD activity occurs in PGPB and contributes to promoting plant growth (26,102–104), even in environmental conditions that would otherwise hinder the growth of plants. Clear evidence was observed using *Pseudomonas* sp. UW4 strain, displaying the significant root elongation in *Brassica napus* (canola) plants (105), *Burkholderia phytofirmans* (105), *Rhizobium leguminosarum* (100), and *Pseudomonas* spp. (106). The strain (WU–9) induces the antioxidant activity and proline levels in plants and helps the plants to combat salt toxicity (107).

SYNERGY BETWEEN ACCD AND OTHER SALINE STRESS TOLERANCE MECHANISMS

Plant growth is promoted by both direct and indirect mechanisms (44,108). Generally, bacteria that promote plant growth facilitate the uptake of essential nutrients and influence plant hormone levels. Hence, ACCD is considered to be a direct mechanism for encouraging plant growth (8).

PGPB mechanisms have previously been explained concerning how IAA and ACCD promote plant growth (102,103) and interact with other plants to promote plant growth in different ways. Inoculating plants with bacterial consortia has been shown to benefit plants in a better way than inoculating the plants with a single bacterium (109). The *acdS*$^{+}$ strain *Pseudomonas* sp. UW4 in conjugation with AM fungus *Gigaspora rosea* has been reported to improve the root length, leaf area, and biomass of cucumber (*Cucumis sativum* L.) plants (110). Previously, Orozco–Mosqueda et al., (2019) generated a series of mutants *Pseudomonas* sp. UW4 in order to evaluate the roles of ACCD and trehalose conferring salt–tolerance on tomato plants. A recent study shows that overexpressing trehalose (*OxtreS*) significantly enhanced the tomato plants' ability to withstand SS compared to the wild–type strain. In line with these results, it has been suggested that both ACCD and trehalose play a role in PGPB–mediated salt tolerance (44,111). It has been observed that if ACCD activity is synergistic with bacterial auxin production its activity is optimized (44). In this manner, PGPB would promote the plant growth directly, as well as indirectly through synergistic actions between the different mechanisms, protecting the plants from salinity and other stresses like flooding, heavy metals, drought, flower wilt, and phytopathogens (27,44).

PGPR–DRIVEN ROS SCAVENGING IN SALINITY STRESS

PGPR employs a complex set of mechanisms to protect plants against SS, which are intricately modulated and linked to one another. Due to SS, nitrogenase activity, as well as its synthesis, gets affected in the osmo–adaptation mechanism of *Azospirillum* species (112). This results in the accumulation of compatible solutes including glycine–betaine, proline, glutamate, and trehalose which play a crucial role in osmoregulation. Salinity stress generates ROS, which includes singlet oxygen (O_2), hydroxyl (OH^-), superoxide ($O2^{2-}$), and hydrogen peroxide (H_2O_2), which promote oxidative stress thereby damaging the cellular structures. Furthermore, excessive ROS production and SS cause severe dehydration in plant cells. Under SS, proline is one of the most important osmoprotectants in plant cells. There is some evidence that PGPR–induced proline content that may serve to maintain a balance between extracellular and intracellular osmotic pressure, thereby improving the ability of cells to hold moisture and managing SS (113). Additionally, stress triggers the antioxidant enzyme system, which acts as a defense mechanism. Non–enzymatic and enzymatic H_2O_2 scavengers are both involved in the antioxidant systems that affect H_2O_2 levels. ROS–mediated oxidative stress can be neutralized by PGPR, which generates antioxidants enzymes, namely catalase (CAT), superoxide dismutase (SOD), ascorbate peroxidase (APX), peroxiredoxin (Prx), glutathione reductase (GR), glutathione peroxidase (GPX), and glutathione S–transferases (GSTs), and non–enzymatic compounds, for example, α–tocopherol, glutathione (GSH), ascorbate (AsA), phenols and flavonoids, including H_2O_2, are regularly involved in controlling the ROS level (**Table 4**) (114).

Plant stress tolerance is not solely dependent on ROS–scavenging non–enzymatic and enzymatic antioxidants, but also ROS–responsive signaling and regulatory genes. According to the study conducted by Bharti and Barnawal (2019), salt tolerance was improved by regulating a wide range of salt mitigating genes including ROS–scavenging enzymes. The over–expression of mitogen–activated kinase kinase–1 (MKK1) in Arabidopsis, enhanced the MAPK cascade activity, (115) leading to improved abiotic stress tolerance by analyzing stress–associated ROS concentrations (114).

PGPR induces stress management and its control at a genetic and signaling level as well as of these interrelated mechanisms by scavenging ROS through antioxidant enzymes, plants can reduce oxidative damage and increase their tolerance to SS. In PGPR inoculated plants under SS, antioxidant genes are likely involved in regulating ROS levels (**Table 5**). These results are in line with earlier studies that showed that PGPR treatment stimulated an antioxidant defense mechanism, decreasing the concentration of ROS in salt–stressed plants (116). Despite extensive research on antioxidant enzyme activities, its impact on salt tolerance is not completely understood, since the antioxidant activity is related to both salt sensitivity and tolerance (117).

Also by enhancing antioxidants and polyamines in salt–affected plants, bacteria moderate the redox state and increase photosynthetic efficiency (118). Although, much remains to be clarified regarding the attributes of inter–related mechanisms

S. No.	Non–enzymatic Antioxidants	Function	Subcellular location	Reference
1.	Ascorbic Acid (AA)	Detoxifies H_2O_2 via the action of APX	Apoplast, cytosol, chloroplast, peroxisome, mitochondria, and vacuole	(119)
2.	Reduced Glutathione (GSH)	Acts as a detoxifying co–substrate for enzymes like peroxidases, and GR	Apoplast, cytosol, chloroplast, peroxisome, mitochondria, and vacuole	(119)
3.	α –Tocopherol	Detoxifies compounds that induce membrane lipid peroxidation.	Mostly in membranes	(119)

Cont. Table 4: Antioxidant Enzymes and their Role in their Sub–Cellular Location

S. No.	Non–enzymatic Antioxidants	Function	Subcellular location	Reference
4.	Carotenoids	LHCs absorb surplus energy from photosystems	Chloroplasts and chromoplasts/ leucoplast	(119)
5.	Flavonoids	Direct scavengers of H2O2 and $^1O_2$ and OH	Vacuole	(119)
6.	Proline	Efficient scavenger of OH and $^1O_2$ and prevent damages due to lipid peroxidation	Cytosol, mitochondria and chloroplast	(119)

Table 4: Antioxidant Enzymes and their Role in their Sub–Cellular Location

H_2O_2– Hydrogen peroxide; APX– Ascorbate peroxidase; GR– Glutathione reductase; LHC– Light harvesting complex.

S.No.	Crops	ACCD containing PGPR	Mechanism	References
1.	Rice	*B. pumilus* and *B. amyloliquefaciens*	Increase in NR activity; transcriptional regulation of antioxidant genes	(50,120)
2.	Wheat	*B. subtilis*	Increase in total soluble sugars and PRP content	(121)
3.	Cucumber	*Burkholdera cepacia* and *Enterobacter* sp.	Reduced activities of CAT, POX, PPO, increased GA; Enhanced amino acids, suppressed SA synthesis	(122,123)
4.	Red pepper	*P. Frederiksbergensis* OS261	Increased CAT and reduced SOD and APX	(124)
5.	Cotton	*Klebsiella oxytoca*	Increasing germination rate and disease control	(125,126)
6.	Chickpea	*M. ciceri*	Improving the symbiotic performance	(127)
7.	Mung bean	*Rhizobium sp.*	Nitrogen fixation and plant hormone regulation	(128)
8.	Pea	*Bacillus* and *Pseudomonas sp.*	ACCD activity, IAA production, modulating the antioxidant defense and cell rescue genes	(26)

Table 5: Effect of acdS Positive PGPR in Ameliorating its Salinity Stress

PRP– Proline; NR– Nitrate reductase; CAT– Catalase; POX– Peroxidase; PPO– polyphenol peroxidase; GA– Gibberellins; SA– Salicylic acid; ACCD– 1–aminocyclopropane carboxylic acid deaminase; IAA– Indole acetic acid.

PGPR FORMULATIONS

The efficiency of an inoculant is determined by its formulation, which can make or break it (129). The active ingredient (microorganisms) is often placed in a carrier environment with chemicals that aid to stabilise and protect the microbial cells throughout storage, transit, and delivery to the target site. (130). A formulation that transfers the growth–promoting efficiency of a strain from the lab to the field would have significant implications for agriculture. Inefficient storage and non–reproducible results in the field are often the most significant barriers to commercializing biofertilizers due to formulation deficiencies (131). Thus, it is imperative to examine both the rate of survival of the immobilized bacteria in the various carriers and their ability to retain their beneficial attributes for plant–growth. The Bureau of Indian standard (BIS) is responsible for formulating the standards for biofertilizers and has specified that all bacterial inoculants should contain 10^8 cfu per ml of liquid inoculants, and 5×10^7 cfu per gm of carrier and should not be contaminated at 10^{-5} dilution (132). In the formulation process, the pH of carriers must be close to neutral in order to ensure the efficacy of the biological agents (131). Inoculants can be transported effectively through materials with high water up–take and good aerating properties. Compared to wet formulations, dry formulations have a longer shelf life, are easier to store and transport, as well as provide extended shelf life. There have been research projects covering the study of several bacterial genera; however, *Pseudomonas* and *Bacillus* have drawn the most funding for the development of bioproducts. Researchers have concentrated on improving the survival of *Pseudomonas* in commercial formulations by exploring alternatives. Additionally, *Bacillus* bacteria have a longer shelf life in commercial formulations due to their resistance to desiccation and heat; this explains why *Bacillus*–based products are common. Such bio–formulation can reduce the use and application of chemical pesticides in the field, and can reduce the health risks for farmers. It can also contribute to improving the environmental impact of agriculture and can help growers to reach a sustainable farming system. Several formulations of *Pseudomonas fluorescens* and *Bacillus subtilis* have been successfully commercialized (132). The organic product market is also gaining popularity among consumers. Due to its inert characteristics and accessible availability from soapstone manufacturers, talc is particularly suitable as a carrier for formulation development. Talc is a natural mineral called soapstone or steatite. It consists primarily of minerals containing chloride and carbonate. The powder forms are available from a wide range of industries, and they are known chemically as magnesium silicate ($MgSi_4O_{10}(OH)_2$). The chemical inertness, reduced moisture absorption, hydrophobicity, and its ability to prevent hydrate bridge formation have enabled it to be stored for longer periods of time (http://www.luzenac.com/food.htm). Gupta et al. (85) in his study evaluated the beneficial effect of charcoal based carrier bioformulation on Pea and Zea mays seed germination.

CONCLUSION AND FUTURE PROSPECTS

Soil salinization is a serious concern in India, posing a threat to food security. It's a dynamic process driven by both natural and human-made variables. SS is dealt with by built-in systems in plants. In many cases, however, these techniques are insufficient to prevent severe stifling of plant growth and development. Fortunately, all plants interact with and are related to rhizosphere bacteria, which influence plant development positively (108). The PGPB genus of bacteria is particularly interesting to agricultural crops because it contains a number of beneficial mechanisms, such as ACCD, which can increase plant tolerance to SS by cleaving ACC, which is a direct precursor of ethylene. The activity of ACCD bacterial strains and their critical importance in reducing ethylene levels in plants under SS, as well as other types of stress, has long been known (26). Chemical and physical treatment of seeds prior to sowing, as well as the application of sustainable agricultural management strategies, are two methods for reducing SS in agriculture that have both helped to alleviate the effects of excessive salt deposition in soil. Without a doubt, using PGPB, especially the group of PGPbacilli that have ACCD activity, is a promising option for increasing the quality and output of agricultural goods in salty soils.

Acknowledgments

Anmol Gupta is like to acknowledge DST–INSPIRE (IF160803) for providing him fellowship assistance.

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How to cite this article:

Gupta A., Singh K., Charles M., Pathak N. Role ofACC Deaminase Producing Plant Growth Promoting Rhizobacteria inAmeliorating the Salinity Stress conditions: A Review. Era J. Med. Res. 2022; 9(1): 60-77.