



# Possible mechanisms for the equilibrium of ACC and role of ACC deaminase-producing bacteria

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## Abstract

Plant growth-promoting rhizobacteria (PGPR) actively colonize the plant rhizosphere, which not only stimulates plants' growth and development but also mitigates the adverse effects of abiotic stressors. Besides other techniques and approaches used for the alleviation of abiotic stress conditions, the utilization of PGPR with multiplant growth-promoting traits is desirable because the application of PGPR is pragmatic, sustainable, and environmentally friendly. In the past four decades, numerous ACC deaminase-producing PGPR have been reported for the improvement of crop plants' growth and development under different abiotic stress conditions. Since 1-aminocyclopropane-1-carboxylate (ACC) deaminase producing PGPR regulates ethylene production by utilizing the exuded ACC, which is an immediate precursor of ethylene biosynthesis. However, little is known about the basic mechanism involved in the acquisition of ACC by ACC deaminase-producing bacteria since the enzyme ACC deaminase is localized inside the bacterial cells and ACC is exuded into the rhizosphere from plant roots. In the present article, we proposed candidate attractants involved in the transfer of ACC into ACC deaminase-producing bacteria. Additionally, we discussed the importance and relation of these candidate attractants with ACC deaminase under abiotic stress conditions.

## Key points

- *The ethylene precursor, ACC, exude from plant tissues under abiotic stresses*
- *ACC deaminase activity of PGPR localized in the cytoplasm and periplasm of bacteria*
- *Proposed candidate attractants for the transfer and equilibrium of exuded ACC*

**Keywords** Plant-microbe interaction · PGPR · ACC deaminase · ACC exudation and transfer · Abiotic stress

## Introduction

The ever-increasing world population growth (estimated current growth 1.1% per year) and its environmental impacts have put a significant pressure on the existing agriculture system around the globe, and it is obvious that global food production may soon be inadequate to feed all of the world's population from the same current resources like agricultural land, water, etc. The proportion of undernourished people increased to 10.6% (2015) and then to 11% (2016) worldwide (Glick 2014; Molotoks et al. 2021). On the other hand, different strategies and approaches are

utilized for increasing crop production: vertical farming; drip irrigation system; greater use of chemicals including insecticides, nematicides, herbicides, and fertilizers; use of transgenic crops and applications of biofertilizers are now being used in higher quantities than the past (Enebe and Babalola 2018; Glick 2014). Definitely, these methodologies have contributed a lot and enhanced agricultural productivity, but some are not sustainable and revealed their adverse effects on the ecosystem. In general, most of the fertilizers and chemicals are nonspecific and may be wasted in the fields or kill the microbes that are beneficial or even harmless to the plant and environment. It has been estimated that about 0.1% of the pesticides and insecticides reach the target organisms, whereas the remaining chemicals contaminate the surrounding environment (Glick 2014; Gill et al. 2014; Carriger et al. 2006). Recently, microbial biotechnology approaches provide the best understanding about plant-microbe interactions and potential applications of plant microbiomes for plant growth promotion and productivity

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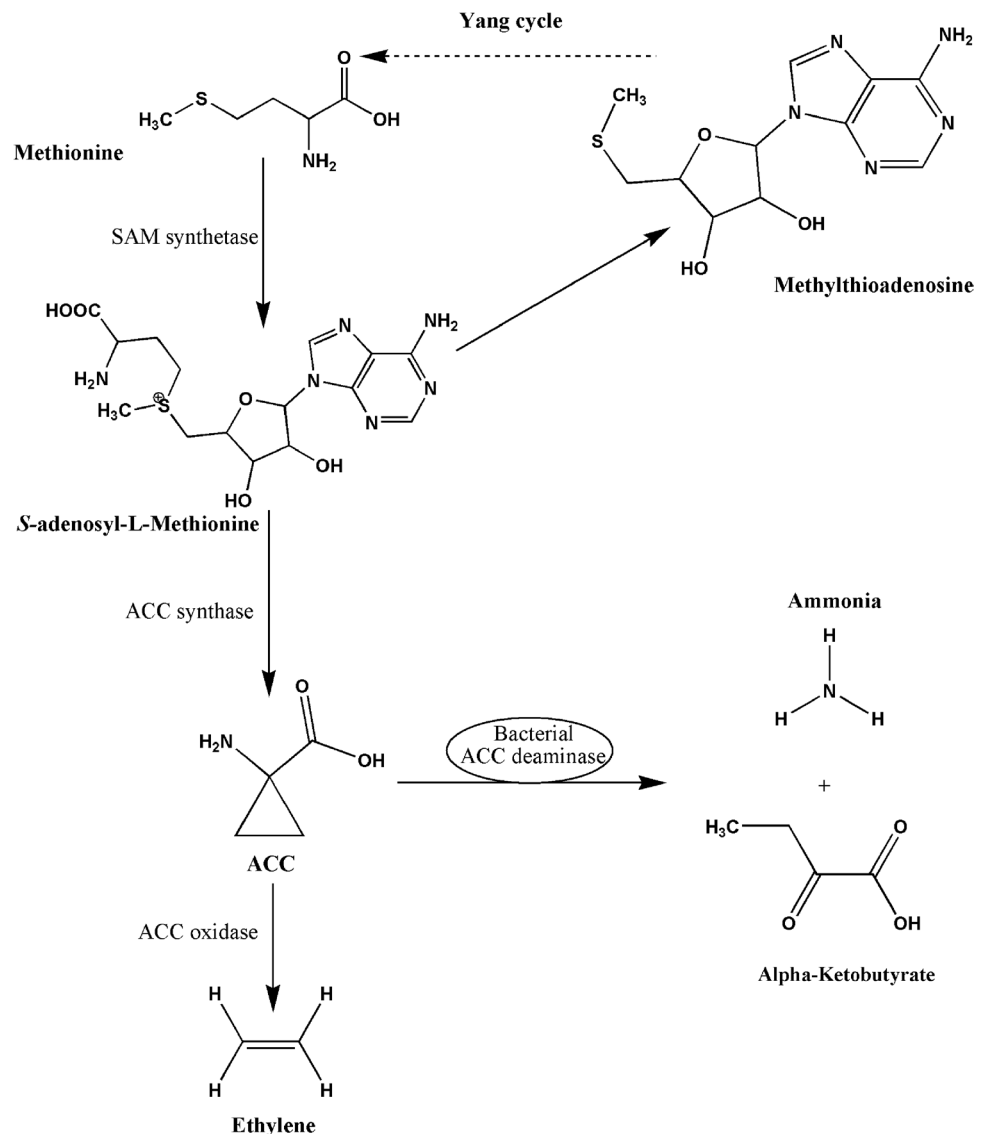
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(Imade and Babalola 2021). Thus, the pragmatic use of ACC deaminase-producing PGPB in agriculture is a logical and sensible technique for sustainable agriculture. This effect has been widely studied and reported (Bano et al. 2021; Glick et al. 2007; Siddikee et al. 2010; Glick 2014; Ali and Kim 2018; Gowtham et al. 2020; Nadeem et al. 2021; Han et al. 2021).

Several different types of PGPB have been identified to date, each with one or more plant growth-promoting traits which may contribute and enhance plant growth by fixing atmospheric nitrogen, siderophores production, synthesis of phytohormones, phosphate solubilization, antibiotic production, ability to act as biocontrol agents against phytopathogens and production of ACC deaminase enzymes (Hassan et al. 2015; Rajkumar et al. 2010; Etesami et al. 2014; Khan et al. 2016). Currently, most of the research groups paved their attention to PGPR with ACC deaminase activities and revealed a number of different PGPR that produce ACC

deaminase, which cleaves ACC (nonprotein amino acid and immediate precursor of the hormone ethylene) and alleviates the levels of stress ethylene produced under abiotic stress conditions (Penrose and Glick 2003; Singh et al. 2015; Li et al. 2019). In normal conditions, methionine is converted into *S*-Adenosyl-L-Methionine (SAM) by SAM synthetase, then ACC synthase converts *S*-Adenosyl-L-Methionine (SAM) to ACC, and then ACC oxidase converts ACC into ethylene inside plant tissues (Fig. 1). Generally, a very low concentration (0.01  $\mu\text{L/L}$ ) of ethylene regulates the growth and development of the plant, however, a higher concentration (20–25 g/L) of ethylene is produced from the excessive amount of ACC produced under abiotic stress conditions (Ali and Kim 2018; Singh et al. 2015). This higher amount of ethylene might be detrimental to the plant and may cause leaf abscission, epinasty, reduction in chlorophyll content, speeding up the aging process, and ultimately death of the

**Fig. 1** Ethylene biosynthetic pathway and role of ACC deaminase producing bacteria. In this pathway, the enzyme SAM synthetase converts methionine to *S*-adenosyl-L-methionine. Then ACC synthase converts SAM into ACC (1-aminocyclopropane-1-carboxylate). In this reaction, methylthioadenosine (MTA) is also produced, which is reconverted to methionine by a series of biochemical reactions, this multi-step pathway is also known as the Yang cycle. The enzyme ACC oxidase converts ACC into plant hormone ethylene. ACC deaminase producing bacteria hydrolyze the exuded ACC into ammonia and  $\alpha$ -ketobutyrate, PGPB alleviate the formation of stress ethylene level under stressful conditions



plant (Grichko and Glick 2001; Ali and Kim 2018; Singh et al. 2015). On the other hand, PGPB with ACC deaminase cleave plant ethylene precursor ACC and lower the level of ethylene in plants under stressful conditions (Table 1).

A bacterium with a low level of ACC deaminase activity ( $\geq 20$  nmol  $\alpha$ -ketobutyrate  $\text{mg}^{-1}\text{h}^{-1}$ ) is sufficient to grow on ACC and to act as plant growth promoting rhizobacteria. Similarly, microorganisms (bacteria and fungi) with higher levels of ACC deaminase activity (300–400 nmol  $\alpha$ -ketobutyrate  $\text{mg}^{-1}\text{h}^{-1}$ ) do not necessarily enhance root elongation or growth promotion to any greater extent compared to the strains that involve less ACC deaminase activity under different environmental conditions (Penrose and Glick 2003). The study of Jacobson et al. (1994) revealed that ACC deaminase activity occurs exclusively in the cytoplasmic compartment of the cells and is never found in the cell growth medium of ACC deaminase-producing bacteria. Their results revealed the cellular localization of

ACC deaminase activity and concluded that ACC deaminase activity can be only found in the cytoplasmic and periplasmic compartments of ACC deaminase-producing bacteria (Jacobson et al. 1994). This cytoplasmic and periplasmic localization of ACC deaminase suggests that if ACC from the plant roots is to be cleft by ACC deaminase-producing bacteria, then ACC must be exuded from plant roots and transported inside the bacterium because the bacterial enzyme (ACC deaminase) is not secreted outside. Thus, substrate ACC must be oozed out from plant tissues and transported into ACC deaminase containing bacteria. Unfortunately, no information is available on the transportation, signals transduction, or molecular communication of the exuded ACC from plant tissues and its entry into ACC deaminase-producing bacteria. There must be an accurate mechanism for the dynamic equilibrium of ACC concentration in the rhizospheric region, their molecular communication, and transportation from plant tissues to the bacterium.

**Table 1** ACC deaminase producing bacteria alleviate abiotic stress conditions

Bacteria	Plants species	Abiotic stress	Reference
<i>Burkholderia pyrrocinia</i> strain P10	Peanut	Salinity stress	Han et al. 2021
<i>Bacillus megaterium</i> , <i>B. tequilensis</i> , and <i>Pseudomonas putida</i>	Wheat	Salinity stress	Haroon et al. 2021
<i>Bacillus velezensis</i> strain D3	Maize	Drought stress	Nadeem et al. 2021
<i>Bacillus cereus</i> KTES	Tomato	Heat stress	Mukhtar et al. 2020
<i>Bacillus subtilis</i> SF 48	Tomato	Drought stress	Gowtham et al. 2020
<i>Bacillus methylotrophicus</i> PM19	Wheat	Salinity stress	Din et al. 2019
<i>Bacillus gibsonii</i> PM11 and <i>Bacillus xiamenensis</i> PM14	<i>Linum usitatissimum</i> L.	Heavy metal stress	Zainab et al. 2020
<i>Burkholderia cepacia</i> and <i>Serratia marcescens</i>	<i>Capsicum annuum</i>	Salinity and drought stress	Maxton et al. 2018
<i>Pseudomonas veronii</i> KJ	<i>Sesamum indicum</i> L.	Waterlogging stress	Ali et al. 2018
<i>Bacillus licheniformis</i> HSW-16	Wheat	Salt stress	Singh and Jha 2016
<i>Pseudomonas fluorescens</i> DR7	Foxtail millet	Drought stress	Niu et al. 2018
<i>Pseudomonas fluorescens</i> SorgP4	Crop plants	Drought stress	Ali et al. 2014
<i>Burkholderia</i> sp. SX9	Ryegrass	Heavy metal stress	Wang et al. 2021
<i>Enterobacter</i> strain G	Pigeon pea	Salinity stress	Anand et al. 2021
<i>Pseudomonas fluorescens</i>	Sweet corn	Drought stress	Zarei et al. 2020
<i>Kosokonia sacchari</i>	Mung bean	Salinity stress	Shahid et al. 2021
<i>Klebsiella</i> sp.	Sunflower	Heavy metal stress	Carlos et al. 2016
<i>Enterobacter</i> sp.			
<i>Pseudomonas stutzeri</i> A1501	Rice	Salinity and heavy metals	Han et al. 2015
<i>Pseudomonas putida</i> CEN7, <i>P. fluorescens</i> CEN8	Rice	Waterlogging	Etesami et al. 2014
<i>Pseudomonas putida</i> HS-2	Canola	Heavy metal stress	Rodriguez et al. 2008
<i>Pseudomonas fluorescens</i> SorgP4	Crop plants	Drought stress	Ali et al. 2014
<i>Pseudomonas fluorescens</i> 913	Wheat	Cadmium stress	Govindasamy et al. 2009
<i>Pseudomonas putida</i> HS-2	Canola	Heavy metal stress	Rodriguez et al. 2008
<i>Rhizobacteria</i> isolate SAN1	Wheat	Cadmium stress	Hassan et al. 2016
<i>Klebsiella</i> Sp. strain SBP-8	Broom-corn	Salinity and heat stress	Singh et al. 2015
<i>Pseudomonas fluorescens</i>	Chinese cabbage	Salinity stress	Soh et al. 2014

Comprehensive research activity is required to explain the dynamic equilibrium of ACC in the root, rhizosphere, and bacterium. Initially, Glick et al. (1998) presented a model for lowering plant ethylene concentrations by ACC deaminase-producing plant growth promoting rhizobacteria (PGPR). Their study suggested that PGPR stimulates the growth of the plant by producing indoleacetic acid (IAA), ACC deaminase, and lowering the levels of stress ethylene. The exuded ACC is taken up ACC deaminase-producing bacteria and hydrolyzed to ammonia and  $\alpha$ -ketobutyrate (Fig. 1). The model revealed that the availability of ACC to the bacterium is based on the concentration gradient, and the plant must exude a higher amount of ACC to maintain the equilibrium between internal and external ACC levels (Glick et al. 1998). However, rhizosphere and rhizobacterial interaction depend on plant root exudates, which consist of various organic compounds that attract the bacteria for robust colonization in rhizosphere and rhizoplane regions. The study of Li et al. (2019) revealed that ACC is the strongest chemoattractant for ACC deaminase-producing PGPR, and the chemotactic mobility of bacteria is based on essential signaling molecules when these signaling components are absent, the bacterial chemotaxis does not take place (Li et al. 2019). ACC being a common exudate from seeds and roots under abiotic stress conditions whereas, a common substrate for ACC oxidase and ACC deaminase. Both of these enzymes compete for ACC, and the levels of stress ethylene in plants under stressful conditions are reduced if ACC deaminase reacts earlier than the induction of ACC oxidase (Glick 2014; Ali and Kim 2018). The induction of ACC deaminase before ACC oxidase is completely based on the sensitivity of the stress because bacteria are more sensitive than plants and induce the production of ACC deaminase enzymes. Similarly, other messengers and transporters which may be involved in the transportation of ACC into bacteria are also released in the rhizospheric region.

In the present review, we proposed possible mechanisms for the dynamic equilibrium of ACC in the plant root, rhizosphere, and bacterium and suggest candidate attractants such as exopolysaccharides (EPS), chelators, peptides, and hormones for the transportation of ACC into ACC deaminase producing bacteria. The novelty of the present work is based on the lack of such information in the available literature. Hence, this information is pivotal for researchers utilizing ACC deaminase-producing PGPR as microbial biostimulants or biofertilizers.

### ACC transport and ACC deaminase under abiotic stress

ACC executes a key role in different physiological processes, and the spatial and temporal response of plants to ethylene requires a balanced amount of ACC under different

conditions. The level of ACC is regulated by complex interactions during its production, modification, and transport under stressful conditions. Under waterlogged conditions, ACC is not converted into ethylene due to a lack of molecular oxygen. Thus, ACC is transported from the roots to the shoots via xylem of the plant, where ACC is converted into ethylene by ACC oxidase (Olsen et al. 1995; Poel and Straeten 2014). Similarly, the transport of ACC has also been suggested during other stresses such as drought, salinity, and nutritional deficiency stress and is widely studied (Poel and Straeten 2014; Barnawal et al. 2012; Ghanem et al. 2008). Additionally, ACC can be transported via phloem to other aerial parts of the plant. In cotton plants, the foliar application of radioactively labeled ACC was transported through the phloem (Else and Jackson 1998). The actual mechanism by which ACC is attained and transported by xylem and phloem still needs to be confirmed. Moreover, ACC is also exuded from plants roots in the rhizosphere, and ACC deaminase producing PGPR are attracted by exuded ACC and colonize in the rhizospheric region.

Initially, Honma M and Shimomura T (1978) discovered ACC deaminase in soil microorganisms (*Pseudomonas* Sp. and *Hansenula saturnus*) and revealed to convert ACC to ammonia and  $\alpha$ -ketobutyrate. They also suggested that the molecular weight and *K<sub>m</sub>* value of the enzyme vary with the source organism and require pyridoxal phosphate for its normal activity (Honma and Shimomura 1978). Afterward, the study of Jacobson et al. (1994) reported that ACC deaminase is produced inside a bacterial cell, and 100% of its activity is localized in the cytoplasm. Their results for the localization of ACC deaminase also suggest that the substrate ACC must be transported inside bacteria before it is hydrolyzed. They compared the activity of ACC deaminase with other two marker enzymes: alkaline phosphatase (activity 91.8% localized in the periplasmic region) and Glucose-6-phosphate dehydrogenase (activity 88.6% localized in the cytoplasmic compartments) of ACC deaminase producing bacteria (Jacobson et al. 1994). Similarly, the production of ACC deaminase can be induced on the availability of higher ACC concentration which is a slow and complex process. Therefore, ACC deaminase can be classified as an inducible enzyme localized inside a bacterial cell and the minimum level of ACC for induction was measured as 100 nM in a cell free extract (Singh et al. 2015; Jacobson et al. 1994). Moreover, several studies revealed that a plant in response to biotic and abiotic stress conditions augment the level of plant hormone ethylene which is also detrimental to the plant growth and initiate processes like chlorosis, leaf abscission, and senescence (Liu et al. 2020; Glick et al. 1998; Glick et al. 2007). The hydrolysis of excessive ACC by ACC deaminase-producing PGPR is pivotal to abiotic stress relief.

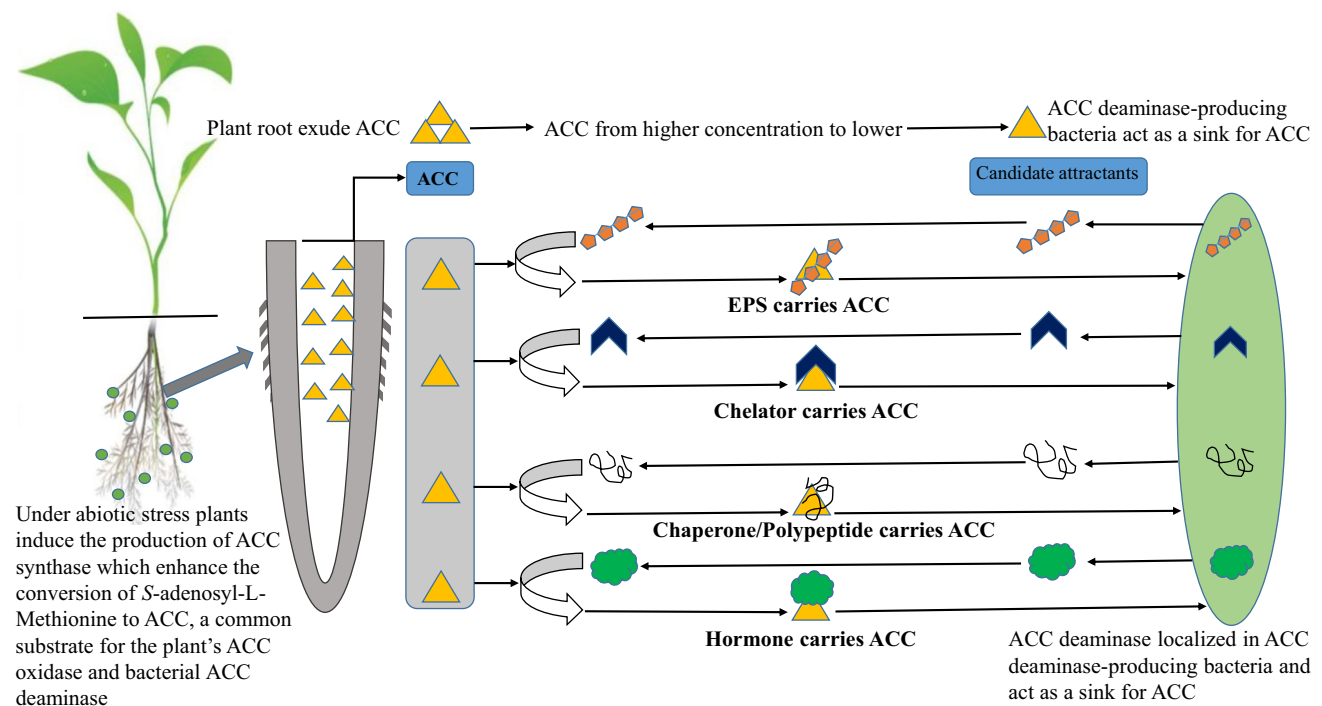
Table 1 summarizes the studies published on ACC deaminase-producing bacteria and their prolific effects on plants

under abiotic stress. Bacteria with ACC deaminase can use ethylene precursor ACC as a source of nitrogen, and the hydrolysis of ACC leads to a decrease in plant ethylene levels. The decrease in stress ethylene level results in increased root growth of the host plant (Glick 2014; Han et al. 2021; Glick et al. 1998). Plant hormone ethylene and its precursor (ACC) play a key role in stress-related signal transduction pathways under abiotic stress conditions. Under abiotic stress, plants augment the production of ACC and stress ethylene, whereas, the decrease in the level of stress ethylene alters the general status of the plant (Nascimento et al. 2018; Tao et al. 2015). More studies are required to understand the mechanism responsible for the transfer of exuded ACC into ACC deaminase-producing bacteria.

### Possible mechanisms for ACC transfer to rhizobacteria

Almost no authentic information is available in the literature on the transfer of ACC to ACC deaminase-producing bacteria. Previously, Glick et al. (1998) proposed that the higher concentration of ACC produced inside plant roots might be exuded from the roots, and ACC deaminase-containing bacteria could act as a sink for exuded

ACC (Fig. 2). Their study was based on the concentration gradient of ACC that more ACC molecules would be secreted from plants tissues to maintain equilibrium in plant tissues, rhizosphere, and ACC deaminase-producing bacteria. The proposed transfer of ACC was solely based on the concentration gradient, and the hydrolysis of ACC maintains a low level of ACC concentration inside ACC deaminase-containing bacteria, which allows a continuous supply of ACC from plant roots to the bacteria (Glick et al. 1998). On the other hand, recent studies revealed ACC as a strong chemoattractant for PGPR that contains *acdS* gene encoding for ACC deaminase. An effective PGPR needs to be compatible in the environment, where root exudates pave the way for rhizosphere colonization, microbes reproduce and form biofilm in the near vicinity of the roots (Li et al. 2019). Similarly, the study of He and Bauer (2014) revealed that Gram-negative species utilize variations in chemotaxis signaling cascade to switch lifestyles in order to survive under different environmental stress conditions, and bacterial chemotaxis is subjected toward higher concentrations of life-sustaining nutrients which involve sensing a gradient of chemicals as small as a few molecules and moving in response to the signals for robust lifecycle. In other words, the chemosensory pathways of bacteria allow them to tune their responses to



**Fig. 2** Proposed mechanisms for dynamic equilibrium of ACC in plant root, rhizosphere, and bacterium under stressful conditions. A cartoon of a root is shown where the transfer of exuded ACC under stressful conditions is transferred into ACC deaminase-producing bacteria; the possible ways for ACC transfer to the bacterial cell may

be based on the concentration gradient, chelators, exopolysaccharides (EPS), peptides/chaperons, or hormones. The signal transduction system regulates different adaptive events in bacteria and may perceive the stress earlier than the host plant and could induce the production of signaling molecules

specific environments (Wadhams and Armitage 2004; Li et al. 2019; He and Bauer 2014).

Thus, bacteria must be able to respond to a changing environment through proper signaling, and bacteria with ACC deaminase acting as a sink for ACC must not merely be based on the concentration gradient of ACC exuded from the plant tissues but adopt a consistent pathway to bring the exuded ACC into ACC deaminase producing bacteria. In the present article, we propose different strategies adopted by ACC deaminase producing bacteria to bring and hydrolyze the exuded ACC under stressful conditions. We propose mechanisms for the dynamic equilibrium of ACC in the plant root, rhizosphere and bacterium, and suggest candidate attractants such as EPS, chelators, peptides and hormones for the transportation of ACC into ACC deaminase producing bacteria (Fig. 2).

EPS are secreted by PGPR to protect themselves and their host plant against abiotic stress conditions while PGPR with ACC deaminase and EPS activity are important to induce stress tolerance in plants (Morcillo and Manzanera 2021; Nadeem et al. 2021). Bacteria can survive under stressful conditions by producing EPS which helps to attach and colonize bacteria to the roots of the host plant (Ali et al. 2014). Bacterial EPS have a high potential application to mitigate salinity and drought stresses in different plants due to their capability of chelating free sodium ions from the soil and halt availability to the plants, and supporting the formation of biofilm, which retains the water layer around roots and improves cell adhesion. Thus, the production of EPS can be used as a simple criterion for the isolation of stress-tolerant microorganisms. Drought tolerant bacteria are capable of producing EPS which support plant germination and growth under drought stress conditions, and rhizobacteria producing EPS and ACC deaminase greatly mitigate the adverse effects of stressful conditions (Niu et al. 2018). The ability of inoculum to colonize and outcompete with other microorganisms in the rhizosphere is a critical step for successful application under stressful conditions because bacteria cannot tolerate extreme stressful conditions.

EPS producing PGPR mediates physiochemical and hydrological changes in the rhizospheric soil, which may help in host plant tolerance and EPS maintains a hydrated microenvironment around bacteria which promotes bacterial communication and survival under drought and salinity stress conditions (Roberson and Firestone 1992). Despite the influence of EPS in the rhizospheric region, little is known about the potential direct impact of EPS composition in plant physiology and communication of EPS producing PGPR and their microenvironment. Interestingly, the production of EPS and hydrolysis of ACC are boosted with an increase in heat stress conditions in tomato plants inoculated with *Bacillus cereus* (MK784894.1), which significantly mitigated the adverse effects of heat stress on the plants. Bacteria such as

*Pseudomonas* and *Bacillus* can tolerate stressful conditions due to the production of EPS which protects them from abiotic stress conditions by regulating the diffusion of organic carbon sources. This effect has been widely studied (Haroon et al. 2021; Zainab et al. 2020; Din et al. 2019; Nandal et al. 2005; Sandhya et al. 2009; Mukhtar et al. 2020; Maxton et al. 2018; Singh and Jha 2016). PGPR also enhances the production of EPS at a low temperature (0–15 °C). The study of Mishra et al. (2011) reported psychrotolerant *Pseudomonads* to have the ability to produce a higher amount of EPS under low temperature (8 °C), and significantly enhance plant biomass and nutrient uptake as compared to untreated control plants (Mishra et al. 2011). EPS can be found in different structural variations by adopting combinatorial arrangements of side chains, functional groups, bonding and linkages, and noncarbohydrate substituents. Almost all rhizobacteria produce EPS, however, the variations in EPS greatly depend upon the type and amount of carbon source available, the type of abiotic stressor, and the growth phase of the bacterium during which EPS synthesis takes place (Gupta and Diwan 2017). Based on the above discussion and the role of EPS in diverse environmental conditions, we propose EPS as a candidate attractant for the transportation of exuded ACC from plant tissues into PGPR with ACC deaminase in the cytoplasmic compartments.

PGPR is capable of relieving the toxicity of metals to different plants by acting on their bioavailability through the secretion of chelators (with a low molecular weight 500–2000 Dalton), also known as siderophores. Siderophores are defined as low molecular weight organic chelators with a high and specific affinity for metals. Presently, almost five hundred compounds are identified as siderophores. PGPR exude these materials in the rhizosphere and make metal elements in the soluble form, which are then absorbed by plant root with a special mechanism (Boukhalfa and Crumbliss 2002; Rajkumar et al. 2010; Zarei et al. 2020). The study of Zarei et al. (2020) reported four PGPR strains (*Pseudomonas fluorescens* P1 (MT949838), *P. fluorescens* P3 (MT949840), *P. fluorescens* P8 (MT949845), *P. fluorescens* P14 (MT949851)), and their synergistic effects in the production of ACC deaminase, auxin, and siderophores which significantly improved the yield traits of sweet corn (Zarei et al. 2020). In plant-bacteria interactions, siderophores are beneficial to plant in mobilizing metal ions, whereas, siderophores and ACC deaminase producing bacteria mitigate the adverse effects of heavy metal stress (Carlos et al. 2016; Etesami et al. 2014; Wang et al. 2021; Anand et al. 2021; Shahid et al. 2021). Dimkpa et al. (2009) reported siderophore synthesizing bacteria in the presence of metals ions paves the way for higher IAA synthesis and revealed that both ACC deaminase activity and IAA synthesis were higher with the Pb, As, and Cu treatments (Dimkpa et al. 2009). Taking into consideration the

above information, PGPR communicates with outer environments, and chelators could be considered candidate attractants for the transportation of ACC into PGPR. Additionally, in a recent study, Kumar et al. (2021) suggested that the consortium of ACC deaminase producing bacteria (*Pseudomonas* sp. TR15a (MW682304.1)) and siderophore producing bacteria (*B. aerophilus* TR15c (MW682306.1)) could play a prominent role in enhanced Cu uptake, improvement of biomass and plant stress tolerance (Kumar et al. 2021).

Abiotic stress factors have a significant influence on the performance of PGPR, and adaptation of PGPR to stressful conditions is a complex process in which different gene functions may be regulated (Srivastava et al. 2019; Grover et al. 2011). As we have already discussed, the prolific role of EPS which protects PGPR from hydric stress and fluctuations in water potential. Similarly, bacteria respond to a sudden increase in temperature by inducing the synthesis of specific polypeptides. These polypeptides are also known as heat shock proteins (HSPs) which consist of molecular chaperones. The bacteria under higher temperatures induce the production of HSPs, and the activity of such a protein is pivotal for cell survival and recovery during high temperatures. Furthermore, the synthesis of cryoprotective polypeptides is induced by cold tolerant-bacteria during extreme low temperature (12 °C) conditions (Koda et al. 2001; Ali et al. 2009; Grover et al. 2011). The study of Munchbach et al. (1999) provided evidence that the presence of chaperones is not restricted to some of the bacteria but might be widespread in the *rhizobiaceae*, which consist of multiple subgroups that greatly contribute to the growth and development of plants (Munchbach et al. 1999). Taking into account the above information, PGPR encodes for different polypeptides through which bacteria communicate with the outer environment and tolerate harsh environmental conditions. We propose peptides/chaperones as candidate attractants for the transportation of exuded ACC from plant tissues into PGPR under stressful conditions.

PGPR that feeds on root exudates of plants can enhance plant growth and development by various mechanisms, and a key trait of various PGPR species is the ability to produce ACC deaminase and act as a sink for exuded ACC (Glick 2014; Saleem et al. 2018). Plant root exudates consist of a large amount of different compounds (organic acids, sugar, and amino acids), and PGPR uses these compounds as a food source, which is the only reason for the higher number of bacteria in the near vicinity of the plant roots. It is estimated that the number of bacteria around the roots of the plants is 10–1000 times higher than in the bulk soil, and in response to the presence of different compounds bacteria synthesize and secrete different bioactive compounds important for host plants. Plant roots exude tryptophan in the rhizospheric region which is taken by IAA producing PGPR, the bacteria in the rhizosphere synthesize and secrete

the phytohormones, which support plant cell proliferation and induce the production of ACC synthase that augment the production of ACC. The exuded amount of ACC needs to be transported into PGPR to be hydrolyzed by the ACC deaminase enzyme, which is localized inside the bacterial cell. Thus, it is proposed here that the hormones produced by PGPR and their communication with plant roots may aid in the transportation of ACC inside the bacterial cell because the enzyme ACC oxidase is localized inside plant tissues and ACC deaminase is localized inside the bacterial cell, and both compete for their common substrate ACC. If ACC deaminase reacts before the induction of ACC oxidase, the reaction paves the way for lowering the levels of higher ACC exuded from plant tissues. The minimum level of ACC for induction of ACC deaminase was measured as 100 nM in *Pseudomonas*, and the Km value of the enzyme extracts at pH 8.5 range from 1.5 to 17.4 mM in different microorganisms. Based on such a low affinity of ACC deaminase for ACC, it was also reported that the availability of ACC induces the activity of the enzymes within the first few hours, which gradually decreases after the initial induction. Additionally, the activity of ACC deaminase was reported over a wide range of pH and temperature in different bacterial species, and the highest activity was observed at pH 8.0 to 8.5 and 30 °C (Saleem et al. 2018; Zhao et al. 2003; Glick 2104; Jacobson et al. 1994; Singh et al. 2015).

## Colonization of ACC deaminase producing bacteria

PGPR interactions and colonization with their host plants is a complex phenomenon and needs to be investigated from different standpoints. The bacteria with multiple growth-promoting traits such as the production of phytohormones (IAA, GAs, and cytokinins), solubilization of phosphate, production of siderophore, and ACC deaminase would greatly contribute to the growth and development of the host plant. Additionally, some PGPR opposes and show an antagonistic effect toward phytopathogens by producing different antibiotics, cellulolytic enzymes or by inducing systemic defense response. Thus, colonization of bacteria in the rhizosphere region is the most important step toward the robust effects of plant and microbe interactions (Nelson 2004; Glick 1995; Bhattacharjee et al. 2012). Colonization of PGPR is based on bacterial swarming and chemotaxis toward the exudates of the plant roots because root exudates are a rich source of nutrients. The study of Li et al. (2019) revealed ACC as a key chemoattractant for ACC deaminase-producing bacteria and concluded that the colonization of PGPR in the rhizospheric region is based on the interaction of PGPR and ACC from host plant roots (Li et al. 2019).

Additionally, PGPR mutants without *acdS* gene and ACC deaminase do not stimulate root elongation but also have significantly reduced colonization ability in the rhizospheric region (Li et al. 2000; Sun et al. 2009). Contrary to this, PGPR which is genetically modified and expresses an exogenous *acdS* gene, revealed a high PGP proficiency with a low inoculum concentration in the rhizospheric region (Li et al. 2000; Holguin and Glick 2001). The study of Etesami et al. (2014) reported the prolific role of ACC deaminase-producing *Pseudomonas fluorescens* strain REN1 (KF731833.1) in colonization and alleviation of stress ethylene of rice seedling under gnotobiotic conditions (Etesami et al. 2014). PGPR colonizes and promotes plant growth through various direct mechanisms such as the production of growth regulators, solubilization of nutrients, nitrogen fixation, etc., or by indirect mechanisms such as removal of phytotoxic substances and stimulation of mycorrhizal development (Bhattacharyya and Jha 2012). The root nodulation of legumes and colonization of arbuscular mycorrhizal fungi are greatly affected by the increased level of ethylene under stressful conditions. On the other hand, ACC deaminase-producing bacteria alleviate the biosynthesis of stress ethylene and improve nodulation and colonization of arbuscular mycorrhizal fungi (Nukui et al. 2000; Ma et al. 2003; Gamalero et al. 2008; Barnawal et al. 2013). Thus, bacteria with ACC deaminase not only colonize efficiently but also stimulate the colonization of mycorrhizal symbiosis in the near vicinity of the host plant.

## Conclusion and future prospects

In the past four decades, researchers have reported a plethora of PGPR with ACC deaminase that mitigate the adverse effects of abiotic stressors and enhance plant growth and development. While a lot more research remains to be done on the understanding of basic mechanisms involved in ACC exudation and transfer to the bacterium. Some of the researchers revealed that the transfer of ACC is based on the concentration gradient, and ACC molecules would be continuously oozing out from plant tissues, a region of higher concentration of ACC, to maintain an equilibrium in the rhizosphere and ACC hydrolyzing bacteria where the concentration of ACC is low. Conversely, it is evident that the chemosensory pathways of PGPR allow them to respond to specific environments, and ACC deaminase-producing bacteria are attracted by ACC being a strong chemoattractant for PGPR with ACC deaminase.

The acquisition of exuded ACC required a proper mechanism and signaling pathways, unfortunately little is known about the transfer of ACC into ACC hydrolyzing PGPR. In the present article, we proposed candidate attractants and their unique strategies for the transfer of exuded ACC into

ACC deaminase-producing bacteria. EPS may be one of the strong candidates for the transfer of ACC into PGPR with ACC deaminase because almost all rhizobacteria produce EPS, and the production of EPS and hydrolysis of ACC are enhanced under stressful conditions. Additionally, EPS maintains a hydrated microenvironment around bacteria and promotes bacterial communication with the outer environment, and sustains bacteria survival under stressful conditions. Similarly, PGPR with ACC deaminase and siderophores alleviate the adverse effects of heavy metal stress. Siderophores synthesizing bacteria augment the production of IAA synthesis and ACC deaminase under stressful conditions, which support the concept of siderophores as a candidate attractant for ACC. However, a detailed study is required to manifest the involvement of siderophores in the transformation of ACC into ACC deaminase-producing bacteria. Furthermore, the fluctuation in temperature induces the synthesis of polypeptides and molecular chaperones which are greatly involved in the survival and recovery of PGPR with ACC deaminase under extreme temperature. HSPs and cryoprotective polypeptides enhance bacterial tolerance of extreme temperature and are prevalent in *rhizobiaceae*. Thus, polypeptides/chaperons may be considered candidate attractants and tools for the transportation of ACC into ACC deaminase-producing PGPR. Similarly, the crosstalk of IAA, ACC, and ACC deaminase pragmatizes the concept of hormones involved in the facilitation/transportation of exuded ACC into PGPR with ACC deaminase.

The presence of ACC hydrolyzing enzyme (ACC deaminase) has been reported in bacteria, eukarya, and archaea, but the activity is known to be present mainly in different species of bacteria and ubiquitous in the PGPR. A plethora of ACC deaminase-producing PGPR has been reported for their prolific effects on plants under stressful conditions. Nevertheless, a lot more basic research is to be done on the understanding of the proper mechanism of signaling pathway and transfer of exuded ACC. Thus, future research should be focused to explain the mechanism involved in the transfer of ACC and acquisition of ACC by ACC deaminase-producing bacteria. This will greatly contribute to utilizing ACC deaminase-producing PGPR as microbial biostimulants or biofertilizers.

**Author contribution** All authors listed have made a substantial, direct, and intellectual contribution to the work and approved the manuscript.

## Declarations

**Ethics approval** This article does not contain any studies with human participants or animals performed by any of the authors.

**Conflict of interest** The authors declare no competing interests.



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