Indole-3-Acetic Acid and 1-Aminocyclopropane-1-Carboxylate Deaminase: Bacterial Traits Required in Rhizosphere, Rhizoplane and/or Endophytic Competence by Beneficial Bacteria

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Abstract Majority of plants harbor a diverse community of bacteria, which can positively affect host plant growth. Plant-associated bacteria have various plant growth-promoting (PGP) traits. Rhizobacteria are PGP bacteria within rhizosphere that can enhance plant growth by a wide variety of mechanisms like production of phytohormones, siderophore, 1-aminocyclopropane-1-carboxylate (ACC) deaminase and volatile organic compounds, phosphate solubilization, biological nitrogen fixation, rhizosphere engineering, quorum sensing signal interference and inhibition of biofilm formation, exhibiting antifungal activity, induction of systemic resistance, promoting beneficial plant–microbe symbioses and interference with pathogen toxin production. In recent years, interest in the use of plant growth-promoting rhizobacteria (PGPRs) to promote plant growth has increased. The use of PGPRs has steadily increased in agriculture and offers an attractive alternative to replace chemical fertilizers, pesticides and supplements. To act as PGPRs, any bacteria should be able to colonize and survive in the rhizosphere of plants. A competent colonization is essential for PGP effects produced by the bacteria and the important first step in the interaction of bacteria with plants. The purpose of this review was to give an overview on the most important PGP traits involved in plant more colonization. It seems that PGP traits of production of IAA and ACC deaminase may be required for endophytic and rhizosphere competence by PGPRs. In addition, this review indicates that the selected bacterial isolates based on their IAA and ACC deaminase-producing traits have the potential for more colonization of plants. Such bacteria may be used for a sustainable crop management under field conditions. Bacterial IAA together with ACC deaminase increase root

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surface area and length, and thereby provide the plant to have greater access to soil nutrients under different environmental conditions including stress situations. Therefore, proper screening of PGPRs can be useful for future agricultural applications, providing higher production yields, reduced input costs and negative environmental impact due to the use of chemical fertilizers.

Keywords Colonization · PGPR · IAA · ACC deaminase · Plant growth-promoting traits · Rhizosphere

1 Introduction

Food security is one of the fundamental needs that can never be ignored by any society. The extensive increases in both environmental damage due to unsuitable agricultural practices and human population pressure have the unlucky consequence that global food production may soon become inadequate to feed all of the world's people. To supplement the nutritional need, it is therefore essential that agriculture becomes intensive and sustainable. In addition, the agricultural productivity must significantly increase without destroying environment within the next few decades. The development of such a global system for sustainable food production is one of the greatest challenges faced by the humans. To this end, agricultural practice is moving toward a more sustainable and environmentally friendly approach. This includes both the use of transgenic plants and plant growth-promoting rhizobacteria (PGPRs) as a part of conventional agricultural practice (Glick 2012). In both managed and natural ecosystems, PGPRs play a key role in supporting and enhancing plant health and growth (Maheshwari 2010). These bacteria are of interest for application in agriculture as biofertilizers and pesticides (biocontrol), as well as for phytoremediation applications (Bhattacharjee et al. 2008; Berg 2009; Lugtenberg and Kamilova 2009; Weyens et al. 2009). Rhizobacteria colonize plant roots and enhance plant growth through a variety of mechanisms. Based on the area of colonization, these bacteria can be grouped into associative bacteria that include rhizosphere (in the vicinity of root) rhizoplane (on the surface of root) and endophytic bacteria. Plant-associated bacteria isolated from rhizoplane and phylloplane surfaces are known as epiphytes (Andrews and Harris 2000), whereas those isolated from the interior of tissues, which they inhabit without causing harm to the host, are called endophytes (Petrini et al. 1989; Azevedo et al. 2000; Sturz et al. 2000), with some bacterial populations fluctuating between endophytic and epiphytic colonization (Hallmann 1997). There are three basic categories of microbial interactions based on ecology, namely neutral, negative and positive interactions generally exist between rhizobacteria and plants (Whipps 2001). Most of the rhizobacteria are commensals in which the bacteria establish an innocuous interaction with the host plants exhibiting no visible effect on the growth and overall physiology of the host (Beattie 2006). In negative interactions, the phytopathogenic rhizobacteria produce phytotoxic substances such as hydrogen cyanide (HCN)

or ethylene, thus negatively influence on the growth and physiology of the plants (Khalid et al. 2005). In contrast to these deleterious bacteria, some PGPRs isolate can promote plant growth and development either directly or/and indirectly. Direct stimulation includes biological nitrogen fixation, producing phytohormones like auxins, cytokinins and gibberellins, solubilizing minerals like phosphorus and iron, while indirect stimulation is basically related to biocontrol, including antibiotic production, production of siderophores and enzymes and induction of systemic resistance, chelation of available Fe in the rhizosphere, synthesis of extracellular enzymes to hydrolyze the fungal cell wall and competition for niches within the rhizosphere (Zahir et al. 2004; van Loon 2007; Akhtar and Siddiqui 2008; Castro et al. 2009). Associative bacteria as well as endophytic bacteria use the same mechanisms to influence plant growth (Lugtenberg and Kamilova 2009). Since the extensive use of chemical based components can cause unanticipated environmental impacts (including nutrient imbalance, substantial economic loss to the farmers and reducing the population of beneficial microorganisms, disruption and degradation of agroecosystem and decreased soil fertility) and impart pesticide resistance in pests (Ayala and Rao 2002), interest in the use of PGPRs to promote plant growth has been increased in recent years. Based on their ability to stimulate plant growth, it is imperative to develop microbial inoculants for use in agricultural production. Depending on their mode of action and effects, these products can be used as biofertilizers (direct mechanisms) and biocontrol agents (indirect mechanisms). This application can help to minimize dependence on chemical fertilizers, which have adverse effects on the environment, finally leading to have sustainable agriculture and environment (Fig. 1).

PGPRs may use more than one of these mechanisms to enhance plant growth, as experimental evidence suggests that the plant growth stimulation is the net result of multiple mechanisms that may be activated simultaneously (Martinez-Viveros et al. 2010). Despite their different mechanisms of action, their use has not been developed to its full potential due to inconsistencies in their performance and their commercialization has been limited to a few developed countries. In many cases, PGPRs fail to induce the desired effects when applied in the field. This might be due to insufficient rhizosphere and plant colonization, which is as an important step required for exhibiting beneficial effects (Lugtenberg et al. 2001). In addition, the variability in the performance of PGPRs under in vitro and field conditions may be due to various environmental factors that may affect their growth and exert their effects on plant. The environmental factors include climate, weather conditions, soil characteristics or the composition or activity of the indigenous microbial flora of the soil (Chanway and Holl 1993; Zhender et al. 1999). To achieve the maximum growth-promoting interaction between PGPRs and plant, it is important to discover how the rhizobacteria exerting their effects on plant and whether the effects are altered by various environmental factors, including the presence of other microorganisms (Bent et al. 2001). One possible approach is to investigate soil microbial diversity for PGPRs having combination of plant growth-promoting (PGP) activities and well adapted to particular soil environment. Regardless of the mechanism of plant growth promotion, to be more effective in

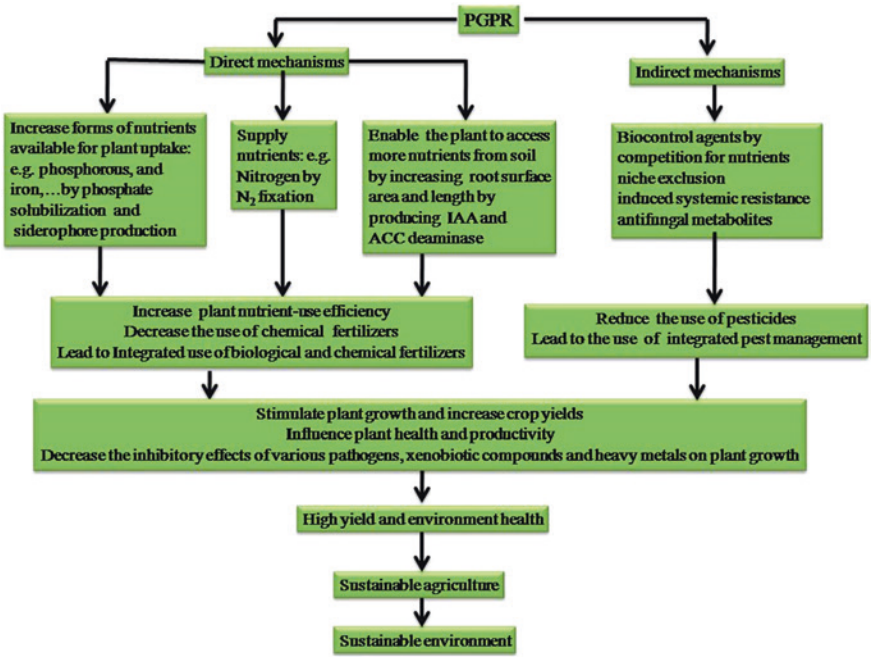

Fig. 1 The role of PGPRs using different mechanisms of action in sustainable agriculture and environment

the rhizosphere, PGPRs must maintain a critical population density for a longer period (Compant et al. 2005). In addition to these traits, PGP bacterial isolates must be rhizosphere/endophytic competence, able to survive and colonize in the rhizosphere soil (Cattelan et al. 1999; Chandra et al. 2007; Martínez-Viveros1 et al. 2010). Therefore, not only mechanisms responsible for plant growth promotion have to be investigated, but also a thorough understanding of all steps involved in plant colonization by PGPRs is required to improve the efficiency and reliability of inoculant isolates. PGP traits can be assessed under laboratory conditions and allow the selection of strains that could lead to increased plant growth (Yanni et al. 1997). Naturally, plants select PGPRs that are competitively fit to occupy compatible niches without causing pathological stress on them. Plant is restricting or directing the development of the attracted organisms in a way to keep control of these guests by excreting quite selective mixtures of substances that provide selective conditions for rhizosphere microorganisms. Furthermore, rhizosphere is a quite heavily populated microhabitat, which is characterized by competition and even predation among the inhabitants. Therefore, soil microorganisms do experience the rhizosphere environment as microhabitat of great opportunities but also of big challenges. The use of epiphytic and rhizosphere bacteria in agricultural production depends on our knowledge of the bacteria–plant interaction and our ability to maintain, manipulate and modify beneficial bacterial populations under

field conditions (Hallmann 1997). The interactions that occur between plants and their associated microorganisms have long been of interest, as knowledge of these processes could lead to the development of novel agricultural applications. However, when screening bacteria for PGP agents, it is better to screen them for the most promising isolates having suitable colonization and PGP traits. In most researches, it has been seen that following incubation, bacterial flora are taken at random from Petri plates or morphological representatives are selected for further study. However, this type of selection may remove some superior bacteria of PGP traits and with high colonization ability. Gram reaction test and other phenotypic characteristics could not definitively determine the classification for the isolates. Therefore, it is essential to study all the bacteria isolated in an economic way. On the other hand, if we test all strains isolated from plants for all PGP traits, this process will take a long time and will be costly. Several methods have been used to demonstrate that root colonization is taking place, including use of fluorescence techniques, antibiotic-resistant mutants and marker genes, such as *LUX* and *GUS*. However, these methods are relatively expensive and time-consuming (Silva et al. 2003). Hence, we were interested in reviewing the previous studies for finding the most important PGP traits in selection of the isolates with more colonization and PGPR potentiality. The studies show IAA can be as a microbial metabolic and signaling molecule in microorganisms, in both IAA-producing and IAA-non-producing species (in plant–bacteria interactions). In addition, the role of bacterial IAA together with 1-aminocyclopropane-1-carboxylate (ACC) deaminase in different bacteria–plant interactions highlights the fact that bacteria use this phytohormone (together with ACC deaminase) to interact with plants as part of their colonization strategy, including phytostimulation and circumvention of basal plant defense mechanisms. It may be suggested that plants select endophytic and rhizosphere bacteria with these traits or that these bacteria harbor other traits that allow them to more effectively reach and establish themselves in rhizoplane and the inner plant tissue. This chapter will focus on the effect of IAA and ACC deaminase-producing bacteria and will provide an insight into plant–bacteria interactions.

2 Plant Growth-Promoting Rhizobacteria (PGPRs)

A diverse group of free-living soil bacteria capable of stimulating plant growth by a number of different mechanisms is known as plant growth-promoting rhizobacteria (PGPRs) (Klopper et al. 1989; Glick 1995) or yield increasing bacteria (YIB) (Tang 1994). The interactions between bacteria and plants may be beneficial, harmful, or neutral for the plant and sometimes the effect of a particular bacterium may vary as the soil conditions change (Lynch 1990). The mechanisms by which these PGPRs increase plant phytohormones, increasing the local availability of nutrients, or facilitating the uptake of nutrients by plants. They also may decrease heavy metal toxicity, antagonize plant pathogens and even induce systemic resistance in the plant against pathogens. This section will focus on plant

growth promotion by PGPRs directly. There are several ways in which PGPRs can directly facilitate plant proliferation (Glick 1995) and they can be distinguished based on the modes of action of PGPRs.

2.1 Providing Nutrients for Plants

Under such conditions, PGPRs can provide the nutrients in soil, which is lacking, such as nitrogen by atmospheric nitrogen (N_2) fixation. Nitrogen (N) is the most vital nutrient for plant growth and productivity. Although, there is about 78 % N_2 in the atmosphere, soil nitrogen is mostly in organic forms and unavailable for plants. The atmospheric N_2 is converted into plant-utilizable forms by biological N_2 fixation (BNF) which changes nitrogen to ammonia by nitrogen-fixing PGPRs using a complex enzyme system known as nitrogenase (Kim and Rees 1994).

2.2 Increasing Nutrients Availability to Plants

A large proportion of nutrients are unavailable for the root uptake by plants, because the nutrients in soils are generally bound to inorganic and organic soil constituents, or alternatively present as insoluble precipitates. Therefore, in these conditions, PGPRs enhance the availability of these nutrients to growing plants by influencing solubility or uptake conditions (such as enhancing the solubility of phosphorus and iron). For example, phosphorus (P) is precipitated after addition to soil, thus becoming less available to plants (Gyaneshwar et al. 2002; Kuklinsky-Sobral et al. 2004). Despite large reservoir of P, the amount of available forms to plants is generally low. This low availability of phosphorous to plants is because the majority of soil P is found in insoluble forms, while the plants absorb it only in two soluble forms, the monobasic ($H_2PO_4^-$) and the diabasic (HPO_4^{-2}) ions (Bhattacharyya and Jha 2012). A considerable amount of phosphorus applied to soil as fertilizers is rapidly fixed into less available forms through complexation with aluminum or iron in acidic soils or with calcium in calcareous soils before plant roots have a chance to absorb it in orthophosphate form (Malboobi et al. 2009). Another PGP activity of PGPRs consists in solubilization of inorganic insoluble phosphates, transforming them into bioavailable forms. Phosphate-solubilizing bacteria (PSB) have been reported for promoting plant growth and increasing yield (Altomare et al. 1999; Barea et al. 2002; Amir et al. 2005; Canbolat et al. 2006; Khan et al. 2009). Secretion of organic acids (production of gluconic acid), proton release or production of chelating substances, exchange reactions and phosphatase enzymes are common mechanisms that facilitate the conversion of insoluble forms of phosphorous to plant accessible forms (Rodriguez and Fraga 1999; Chung et al. 2005; Zaidi et al. 2009; Gulati et al. 2010; Singh and Satyanarayana 2011). Bacteria producing trace element-chelating

organic acids, such as citric, oxalic, or acetic acid have been shown to mobilize various elements in soil (Abou-Shanab et al. 2006; Li et al. 2009). Increased trace element uptake in various plants after inoculation with acid producers or PSB has been reported (Ma et al. 2011a). In aerobic conditions, iron exists primarily as ferric state (Fe^{3+}) and is largely unavailable to plants and microorganisms. Iron bioavailability is also low at neutral pH, as it is mostly in the form of insoluble Fe (III) hydroxides. Siderophores are iron-chelating secondary metabolites, which some PGPRs release under iron-limiting conditions. Siderophore production is widespread among bacteria, which can solubilize and sequester iron, making the nutrient more available to plants. All siderophores possess higher affinity for Fe (III) than for Fe (II) or any other trace element ion (Hider and Kong 2010). In general, soil microorganisms are known to affect the nutrients mobility and availability to the plant, through acidification and redox changes, or by producing iron chelators and siderophores (Burd et al. 2000; Guan et al. 2001; Abou-Shanab et al. 2003).

2.3 Enhancing Plant Greater Access to Soil Nutrients

Nutrient presence in soil and its solubility may be high, but still plants do not have any access to it due to limitations in root growth or activities. Because essential plant nutrients are taken up from the soil by roots (Mills and Jones 1996), good root growth is considered as a prerequisite for enhanced plant development. Therefore, PGPRs enhance the access of plants to the nutrient and more uptake of it by increasing the root growth (such as production of IAA and ACC deaminase). For example, applied N can be lost through nitrate leaching (Biswas et al. 2000). Previous reports have suggested positive impacts of bacteria on N uptake involving non-legume biological fixation (Boddey et al. 1995; Kennedy et al. 1997; Biswas et al. 2000a; Dobbelaere et al. 2001; Saubidet et al. 2002; Wu et al. 2005; Aseri et al. 2008). Many PGPRs cause stimulation of root growth (Biswas et al. 2000, Lucy et al. 2004), sometimes via production of phytohormones by the plant or the bacteria (Lucy et al. 2004; Shaharooma et al. 2008). If promotion of root growth by PGPRs could be achieved with high frequency in the field, PGPR may be potential tools for increasing nutrient uptake (Adesemoye et al. 2009). In general, bacterial IAA and ACC deaminase increase root surface area and length and thereby provides the plant greater access to soil nutrients and water uptake (Vessey 2003; Ryan et al. 2008).

3 Plant–Bacteria Interactions

Plant–bacteria interactions may occur at phyllosphere, endosphere and rhizosphere. Very important and intensive interactions are expected to take place among the plant environment, soil and microflora (Bringhurst et al. 2001). The term

rhizospheric effect designs the fact that bacterial density is higher in the rhizosphere in comparison with non-rhizosphere soil (Foster and Rovira 1978). Although all parts of the plant are colonized by microorganisms, the rhizosphere represents the main source of bacteria with plant-beneficial activities. Biochemical interactions and exchanges of signal molecules between plants and soil microbes have been described and reviewed (Pinton et al. 2007). The plant–bacteria interactions in the rhizosphere are responsible for increasing plant health and soil fertility (Khan et al. 2006). Both aboveground and underground parts of the plants constitute an excellent ecosystem for bacterial activity and development (Bonaterra et al. 2003). The relationship between the PGPRs and their host can be categorized into two basic levels of complexity: (i) rhizospheric and (ii) endophytic. In rhizospheric relationship, the PGPRs can colonize the rhizosphere, the surface of the root or even the superficial intercellular spaces of plant roots (McCully 2001). In endophytic relationship, PGPRs reside within the apoplastic spaces inside the host plants. However, the degree of intimacy between the PGPRs and host plant can vary depending on where and how the PGPRs colonize the plant. PGPRs present in the rhizosphere play important roles in ecological fitness of their host plant. Exploring these bacteria by figuring out their possible relationships with plants, has started a new and fascinating area of investigations in the rhizosphere research. Understanding the interaction between consortium of microbial inoculants and plant systems will pave way to link more benefits from bacterial inoculants for improving plant growth and yield (Raja et al. 2006). Theoretically, the composition of microbes, which colonize the rhizosphere, can be a result of a positive or negative selection procedure or both. In many rhizospheric relationships, the PGPRs are known to colonize the plant root (Andrews and Harris 2000) and exert beneficial effects on plant growth and development by a wide variety of mechanisms.

4 Rhizosphere, Rhizoplane and Endophytic Bacterial Colonization

Root colonization includes the ability of bacteria to establish on or in the plant root, to propagate, survive and disperse along the growing root in presence of the native microflora (Whipps 2001; Lugtenberg et al. 2002; Kamilova et al. 2005; Babalola and Glick 2012). Colonization of bacteria in rhizosphere or on plant surface is a complex process which involves relationship between several bacterial traits and genes due to multistep process. Migration toward plant roots, attachment, distribution along the root as well as growth and survival of the population have all been identified as colonization determinants and have widely been studied in symbiotic, pathogenic and associative plant–microbe interactions. For endophytic bacteria, one additional step is required that is entry into root and formation of microcolonies inter- or intracellularly. Each trait may vary for different associative and endophytic bacteria (Lugtenberg and Dekkers 1999; Benizri et al. 2001;

Rodríguez-Navarro et al. 2007; Compant et al. 2010). The primary colonizers of the bacterial population are strongly influenced by the substances secreted as the root exudates and bacteria benefit from these derive nutrients (Bais et al. 2001; Dakora and Phillips 2002; Walker et al. 2003). Bacteria move toward rhizosphere in response to root exudates, which are rich in amino acids, sugars, organic acids, purines/pyrimidines, vitamins and other metabolic products. In addition to providing nutritional substances, plants start cross talk by secreting some signals which cause colonization by some bacteria while inhibits the other (Bais et al. 2006; Compant et al. 2011). Rhizospheric and/or rhizoplane and endophytic competence are a necessary prerequisite for rhizobacteria to be PGPRs (Compant et al. 2005). The root competence plays a major role in antagonistic activities of some bacteria and is very much essential to deliver the beneficial bacteria at the right place and time on the root, as poor root colonization may result in decreased biocontrol activity (Schippers et al. 1987; Weller 1988; Lugtenberg et al. 1999). Indeed, population size was reported in many works as correlated to the efficiency of biocontrol activity against plant pathogens (Bull et al. 1991). As endophytic PGPRs colonize an ecological niche similar to certain plant pathogens, they are likely candidates for biocontrol agents (Adhikari et al. 2001; Arora et al. 2001; Lacava et al. 2007). Most PGPRs with their efficient PGP potential fail to increase plant yield under field trials in agricultural soils at most of the times. Attempts to exploit PGPRs as biocontrol inoculants, biofertilizers, phytostimulants, or inoculants for bioremediation had limited success so far. This has been attributed to their incompetence to successfully colonize the rhizosphere. In field soil, environmental conditions and competition or displacement by the numerous microorganisms present in the rhizosphere limit colonization (Elliot and Lynch 1984; Thomas et al. 2008). A major factor contributing to inconsistent results from field experiments seems to be variable ecological performance (Somers et al. 2004). Many factors as nature of colonizing organism (bacterial traits), composition of root exudates, bacterial quorum sensing effects, the PGPRs environment, seasonal changes, plant tissue (Bacilio-Jimenez 2003; Mocali et al. 2003), plant species and cultivar, soil type (Kinkel et al. 2000; Fromin et al. 2001; Gnanamanickam 2006; Saleem et al. 2007), sufficient population density, root colonizing ability, PGP ability of the bacteria (Lugtenberg and Dekkers 1999), interaction with other beneficial or pathogenic microorganisms (Araújo et al. 2001; Araújo et al. 2002) and several other biotic and abiotic factors can be involved in rhizosphere and rhizoplane competence by PGPRs (Benizri et al. 2001; Gnanamanickam 2006; Saleem et al. 2007). Further, the phenomenon of chemotaxis, the nature of bacteria flagella (through motility), lipopolysaccharides (LPS) and exopolysaccharides structure, the outer membrane protein *Opr*F and to a lesser extent, presence of pili, all are important for competitive root colonization which determine the colonization of the roots by PGPRs (Lugtenberg and Bloemberg 2004; Fujishige et al. 2006; Böhm et al. 2007). Approaches aiming to enhance PGPRs root colonization have focused on the effect of abiotic factors (Howie et al. 1987) and biotic factors (Notz et al. 2001): host genotype (Baldani and Dobereiner 1980; Smith and Goodman 1999; Adams and Kloepper 2002; Arnold and Lutzoni 2007) and microbial genotypes

(Landa et al. 2002, 2003). Bacteria residing in the rhizosphere of plants may gain access into the root interior and establish endophytic populations. The endophytic colonization of host plant by bacteria reflects on their ability to selectively adapt themselves to these specific ecological niches resulting in an intimate association without any apparent harm to the plant (Sturz and Nowak 2000; Compant et al. 2005a). Exploitation of endophyte–plant interactions can result in the promotion of plant health and can play a significant role in low-input sustainable agriculture applications for both food and non-food crops. An understanding of the mechanisms enabling these endophytic bacteria to interact with plants will be essential to fully achieve the biotechnological potential of efficient plant–bacterial partnerships for a range of applications (Senthilkumar et al. 2011). Successful establishment of the introduced bacteria depends on proper PGPRs selection that must be tailored to the soil and crop combination. There has been considerable confusion over the precise effects of PGPRs, which confounds scientific studies aimed at quantifying their contribution to plant growth. This is largely due to poor understanding of the interactions between PGPRs and their plant hosts and the resident microorganisms, as well as a paucity of information on how environmental factors influence processes that contribute to plant growth promotion (Martínez-Viveros et al. 2010). Therefore, before the deliberate use of PGPRs as biofertilizers or biocontrol agents, it is necessary to know some key parameters such as root colonization capacity, location of infection and degree of persistence of the inoculum (Wiehe and Hoflich 1995). These parameters must be studied under the most realistic conditions possible. The intimacy between plants and environment in rhizosphere is essential for better acquisition of water and nutrients by plants as well beneficial interactions of plants with soil-borne microorganisms (Ryan et al. 2009). Therefore, in this section we will focus on PGP attributes of ACC deaminase and IAA as useful traits in more colonization of rhizosphere, rhizoplane and subsequent endosphere and promoting plant growth (root system) and subsequently more uptake of water and nutrients. For instance, we reported that plant growth promotion observed in rice was more pronounced with endosphere-competent *Pseudomonas fluorescens* as compared to a non-endosphere-competent isolate. This isolate produced both ACC deaminase and IAA (Etesami et al. 2014a). In general, the understanding of colonization processes is important to better predict how bacteria interact with plants and whether they are likely to establish themselves in the plant environment after field application.

5 Indole-3-Acetic Acid (IAA)

A member of the group of phytohormones, IAA is usually considered to be the most important native auxin which influences division, extension and differentiation of plant cells and tissues, stimulate seed and tuber germination, increase the rate of xylem and root development, control processes of vegetative growth and initiate lateral and adventitious roots. Auxins can mediate responses to light and

gravity, florescence, fructification of plants and affect photosynthesis, pigment formation, biosynthesis of various metabolites and resistance to stressful conditions (Tsavkelova et al. 2006). Microbial production of IAA has been known for a long time (Yamada 1993; Costacurta and Vanderleyden 1995; Ludwig-Muller 2004). This property is best documented for bacteria that interact with plants because bacterial IAA can cause interference with many plant developmental processes regulated by this hormone. Many important plant–microbial interactions focus on the production of IAA detected in many pathogenic, symbiotic and free-living bacterial species (Costacurta and Vanderleyden 1995; Tsavkelova et al. 2006). Production of IAA is widespread among a wide range of soil bacteria (estimated to be ~80 % of all soil bacteria) (Khalid et al. 2004), including in streptomycetes, methylobacteria, cyanobacteria and archaea. At present, IAA-producing PGPRs are the most well-studied phytohormone producers (Tsavkelova et al. 2006; Spaepen et al. 2007). These PGP rhizobacteria produce IAA from L-Tryptophan (L-Trp) by different pathways, although it can also be synthesized via L-Trp-independent processes, though in lower quantities (Spaepen et al. 2007). Among PGPRs species, *Azospirillum* is one of the best studied IAA producers (Dobbelaere et al. 1999) and it is generally agreed that IAA production is the major factor responsible for the stimulation of root system development and growth promotion by this bacterium (Spaepen et al. 2007; van Loon 2007). Other IAA-producing bacteria belonging to *Aeromonas* (Halda-Alija 2003), *Azotobacter* (Ahmad et al. 2008), *Bacillus* (Swain et al. 2007), *Burkholderia* (Halda-Alija 2003), *Enterobacter* (Shoebitz et al. 2009), *Pseudomonas* (Hariprasad and Niranjana 2009), *Variovorax* (Belimov et al. 2005; Jiang et al. 2012) and *Rhizobium* (Ghosh et al. 2008) genera have been isolated from different rhizosphere soils. Inoculation with IAA-producing PGPRs has been used to stimulate seed germination, to accelerate root growth and modify the architecture of the root system and increase the root biomass. The ability to synthesize IAA is responsible for symbiotic associations and pathogenesis as well (Patten and Glick 1996; Khalid et al. 2004). A positive correlation between IAA production and growth-promoting activity of diverse PGPRs has been also reported in some plants (Asghar et al. 2002; Khalid et al. 2004; Etesami et al. 2013, 2014b). The root exudates and root-associated microflora are environmentally controlled sources of the IAA influx into the rhizosphere (Kravchenko et al. 1994; Muller et al. 1989; Benizri et al. 1998; Siciliano et al. 1998; Patten and Glick 2002; Badri and Vivanco 2009). Different IAA concentrations have diverse effects on the physiology of plants with plant responses being a function of the type of plant, the particular tissue involved, and its developmental stage. The actual effective range of IAA concentrations varies according to plant species and the sensitivity of the plant tissue to IAA; levels below this range have no effect, whereas higher concentrations inhibit growth (Peck and Kende 1995). For example, Evans et al. (1994) found that only exogenous concentrations between 10^{-10} and 10^{-12} M stimulated primary root elongation in *Arabidopsis thaliana* seedlings. Moreover, the endogenous pool of IAA in the plant is affected by soil microorganisms able to synthesize this phytohormone, and also the impact of bacterial IAA on plant

development ranges from positive to negative effects according to the amount of IAA available to the plant and to the sensitivity of the host plant to the phytohormone. In addition, the level of IAA synthesized by the plant itself may be important in determining whether bacterial IAA will stimulate or suppress plant growth. In plant roots, endogenous IAA may be suboptimal or optimal for growth (Pilet and Saugy 1987) and additional IAA from bacteria could alter the such amount resulting in plant growth promotion or inhibition, respectively (Martínez-Morales et al. 2003; Spaepen et al. 2007). IAA biosynthesis in bacteria is affected by a number of factors including environmental stress, pH, osmotic and matrix stress, carbon starvation and the composition of the root exudates. However, due to the diversity of IAA expression and regulation according to the biosynthetic pathways and bacterial species, all of these factors cannot easily be integrated into a comprehensive regulatory scheme of IAA biosynthesis in bacteria (Spaepen et al. 2007). In general, the production of IAA seems to be one of the most prevalent PGP traits among PGPRs.

5.1 IAA and Stimulation of Plant Growth

Plant-associated bacteria can promote plant growth through modulating the level of plant hormones (Glick 1995; Lee et al. 2004; Dodd et al. 2010). Plants respond properly to environmental changes and adapt their physiology by changing hormones (IAA) levels (De Salamone et al. 2005). The ability of bacteria to produce IAA in the rhizosphere depends on the availability of biochemical precursors and uptake of microbial IAA by plant. However, the total amount of IAA produced by the plant and the bacteria should be optimum to promote plant growth. On the other hand, the production of high levels of IAA is often a main trait of plant pathogens (Rezzonico et al. 1998). Based on the integrated IAA levels produced by plant and PGPRs, a detailed examination of action mechanisms of IAA-producing bacteria in the presence and absence of ACC deaminase activity is described below (Fig. 2).

5.1.1 Stimulation of Plant Growth in the Optimal Levels of IAA Without ACC Deaminase Activity

Plants typically exude a large fraction of their photosynthetically fixed carbon through their roots. Depending on the plant species and environmental conditions, the exudated substrates can account for up to 40 % of the dry matter produced by plants. Root exudates generally contain large amounts of sugars, organic acids and amino acids (L-Trp), vitamins, nucleotides, enzymes and other plant metabolites including IAA, which represent an important source of nutrients for microorganisms in the rhizosphere. They also participate in early colonization by inducing chemotactic response of rhizospheric bacteria. Presence of these compounds is

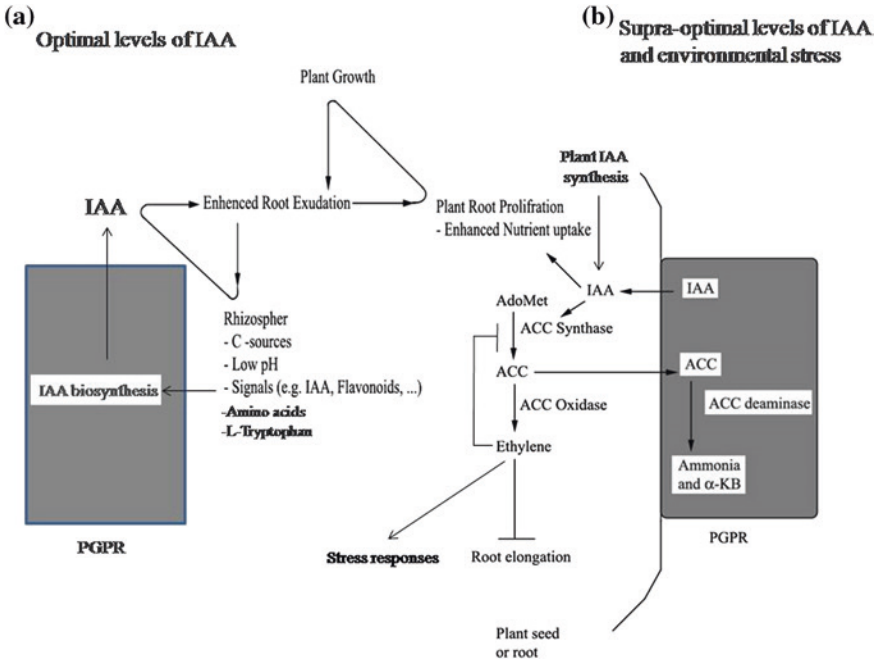

Fig. 2 A possible mechanism of how action mechanisms of IAA-producing bacteria in the presence and the absence of ACC deaminase activity. **a** Stimulation of plant growth in the optimal levels of IAA without ACC deaminase activity. In this case, IAA does not act to stimulate the synthesis of ethylene in the plant. **b** Stimulation of plant growth in the supra-optimal levels of IAA with ACC deaminase activity. In these conditions, IAA acts to stimulate the synthesis of ethylene in the plant. IAA induce the transcription of the plant enzyme ACC synthase that catalyzes the formation of ACC. AdoMet is converted to ACC by the enzyme ACC synthase; ACC is converted to ethylene by ACC oxidase. ACC synthesized in plant tissues by ACC synthase is exuded from plant roots and be taken up by ACC deaminase-producing PGPR. Subsequently, the PGPR hydrolyze ACC to ammonia and α-ketobutyrate. This ACC hydrolysis maintains ACC concentrations low in PGPR and permits continuous ACC transfer from plant roots to bacteria. Otherwise, ethylene can be produced from ACC and then cause stress responses including root elongation. Here, in the absence of ACC deaminase, root-produced ethylene inhibits transcription of IAA response factors, thereby limiting IAA stimulated plant growth as well as IAA promotion of ACC synthase transcription. In the presence of ACC deaminase, ethylene levels are decreased and the obstruction of IAA response factor transcription is alleviated thereby facilitating plant growth. Abbreviations: *ACC* 1-aminocyclopropane-1-carboxylate; *IAA* indole-3-acetic acid; *S*-AdoMet, *S*-adenosy-*L*-methionine. (Modified from Glick (2013) and Lambrecht et al. (2000))

the main reason why the numbers of bacteria in rhizosphere are 10–1000 times higher than in the bulk soil (Glick 2013). Plant-derived IAA presence or adequate amount of IAA precursor molecules in the rhizosphere could be adequate for IAA-producing bacteria to enhance the expression of the *ipd*C gene, involved in IAA biosynthesis (Lambrecht et al. 1999, 2000). An important molecule that can alter the level of IAA synthesis is the amino acid L-Trp, identified as the main precursor

for IAA and thus expected to play a role in modulating the level of IAA biosynthesis. In the rhizosphere, L-Trp is originated from degrading root and microbial cells and from root exudates (Spaepen et al. 2007). In the plant root exudates, PGPRs synthesize and secrete IAA, responding to L-Trp and other small molecules. This IAA, together with endogenous plant-synthesized IAA, can stimulate plant cell proliferation and/or plant tissue elongation (increase of root growth and root length), resulting in greater root surface area. This would enable the plant to access more nutrients from soil (Jacobson et al. 1994; Boiero et al. 2007; Ortiz-Castro et al. 2009) and in turn release more exudates. This IAA can also loosen plant cell walls promoting an increase of root exudation that provides additional nutrients to support the growth of rhizosphere bacteria (James et al. 2002; Chi et al. 2005). The release of more nutrients in turn increases microbial activity and subsequently IAA, and this process continues in a cycle (Fig. 2a).

5.1.2 Stimulation of Plant Growth in the Supra-Optimal Levels of IAA with ACC Deaminase Activity

The majority of substrates for microbial activity in the rhizosphere are derived from the plant. As mentioned above in response to the presence of L-Trp and other small molecules in the plant root exudates, PGPRs synthesize and secrete IAA, some of which is taken up by the plant. The IAA produced from different pathways can induce the transcript of the plant enzyme ACC synthase that catalyzes the formation of ACC. In this case, IAA acts as a stimulator of ethylene in the plant. Along with other small molecule components of root exudates, some of the plant ACC are exuded from seeds, roots, or leaves and may be taken up by the bacteria associated with these tissues, and later cleaved by ACC deaminase (Penrose and Glick 2003) and it can be used as nitrogen (Jacobson et al. 1994; Glick et al. 1995) and carbon sources (Belimov et al. 2005). The cleavage of exuded ACC by bacterial ACC deaminase is eventually acting as a sink for ACC. Moreover, because of lowering either the endogenous or the IAA-stimulated ACC level, the amount of ethylene that could potentially form in the plant is reduced. Subsequently, by lowering plant ethylene levels, ACC deaminase-containing PGPRs can reduce ethylene inhibition in plant growth following a wide range of abiotic and biotic stresses. As a result, plants that grow in association with ACC deaminase-containing PGPRs generally have longer roots and shoots and are more resistant to growth inhibition by a variety of ethylene-inducing stresses. According to Glick (2013) as plant ethylene levels increase, the ethylene that is produced in response inhibits IAA signal transduction, thereby limiting the extent that IAA can activate ACC synthase transcription (Pierik et al. 2006; Prayitno et al. 2006; Czarny et al. 2007; Glick et al. 2007; Stearns et al. 2012). With PGPRs that both secrete IAA and synthesize ACC deaminase, plant ethylene levels do not become elevated to the same extent as when plants interact with bacteria that secrete IAA but do not synthesize ACC deaminase. In the presence of ACC deaminase, there is much less ethylene and subsequent ethylene feedback inhibition of IAA signal

transduction, so that the bacterial IAA can continue to both promote plant growth and increase ACC synthase transcription. However, in this case, a large portion of the additional ACC that is synthesized is cleaved by the bacterial ACC deaminase. The net result of this cross talk between IAA and ACC deaminase is that by lowering plant ethylene levels, ACC deaminase facilitates the stimulation of plant growth by IAA (Fig. 2b).

There are some studies showing IAA and ACC deaminase work in concert to stimulate root elongation. The IAA level affecting the root system ranges from 10^{-13} to 10^{-5} M, depending on the type of root formations (primary or lateral roots, root hairs) and on the plant species (Meuwley and Pilet 1991; Taiz and Zeiger 1998; Dobbelaere et al. 1999). For example, root tissues are more sensitive to fluctuating concentrations of IAA than other plant tissues (Tanimoto 2005). The synthesis of high quantities of IAA by PGPRs has been shown to inhibit the growth of roots rather than to promote it. Primary root growth is stimulated by application of relatively low levels of IAA, typically between 10^{-9} and 10^{-12} M (Alvarez et al. 1989; Meuwley and Pilet 1991; Pilet and Saugy 1987), and is inhibited by higher IAA concentrations, likely by IAA-induced ethylene (Fig. 2b) (Peck and Kende 1995). Production of IAA by *Pseudomonas putida* GR12-2 plays a major role in the root development of canola (*Brassica rapa*) root system as evidenced by the production of roots 35–50 % shorter by an IAA-deficient mutant (Patten and Glick 2002). On the contrary, inoculation of mung bean cuttings with the mutant *aux*1 of the same strain, which overproduces IAA, yielded a greater number of shorter roots compared with controls (Mayak et al. 1999). Treatment of plants with low concentrations (up to 10^{-8} M) of exogenous IAA can enhance nodulation on *Medicago* and *Phaseolus vulgaris*, whereas higher concentrations inhibit nodulation (van Noorden et al. 2006). The combined effect of IAA on growth promotion and inhibition of root elongation by ethylene may be the explanation (Jackson 1991). The bacterial IAA from the plant stimulates the activity of ACC synthase, resulting in increased synthesis of ACC (Jackson 1991), and a rise in ethylene which, in turn, inhibited root elongation (Riov and Yang 1989). Therefore, the production of IAA by itself does not account for the capacity of PGPRs (Xie et al. 1996) in promoting growth. IAA secreted by a bacterium may promote root growth through direct stimulation of plant cell elongation or cell division or indirectly influencing bacterial ACC deaminase activity (Glick 1998; Shah et al. 1998). ACC deaminase hydrolyzes plant ACC and thus prevents the production of plant growth-inhibiting levels of ethylene (inhibitor of root growth) inside the plant because of lack of precursor ACC (Glick 1998, 2005). Mutants of PGPRs that do not produce ACC deaminase have lost the ability to stimulate root elongation (Li et al. 2000), because most IAA knock-out mutants are still able to promote plant growth, IAA biosynthesis alone is not responsible for the overall observed effect (Xie et al. 1996; Dobbelaere et al. 1999, 2003). It is possible that IAA and ACC deaminase work in concert to stimulate root elongation (Jacobson et al. 1994; Li and Glick 2001). In the additive hypothesis, it was suggested that multiple mechanisms, such as IAA biosynthesis, together with ACC deaminase activity, are responsible for the increase in plant growth promotion and yield (Bashan and Holguin 1997; Bhusan et al. 2013). In addition, some PGP traits do not work

independently to each other as exemplified by IAA biosynthesis and ACC deaminase activity. Although bacterial IAA production by some ACC deaminase-containing PGPRs (Glick 1998; Glick et al. 2007a) may stimulate root growth, the creation of bacterial mutants with severely diminished ACC deaminase activity abolished their root growth-promoting effect (Glick et al. 1994; Belimov et al. 2007, 2009). Nevertheless, in vitro application of bacterial mutants with decreased ACC deaminase activity resulted in plants with longer root hairs (Contesto et al. 2008) compared to those inoculated with wild-type ACC deaminase-producing PGPRs. ACC deaminase-containing PGPRs did not affect lateral root development or root architecture in *A. thaliana* (Contesto et al. 2008), *Cucumis sativus* (Gamalero et al. 2008) and *P. sativum* (Jiang et al. 2012). In general, it may be suggested that IAA and ACC deaminase-containing PGPRs can lead to better growth of plants than PGPRs producing ACC deaminase or IAA alone. For example, IAA and ACC deaminase-producing *Variovox paradoxus* 5C-2 stimulated root hair elongation of tomato and pea (*Pisum sativum*) in vitro by producing IAA and decreasing ACC concentrations via ACC deaminase activity (Belimov et al. 2005, 2009a; Belimov 2012; Jiang et al. 2012).

6 IAA as a Signaling Molecule in Bacteria

IAA is important in plant–bacteria interactions and may be involved at different levels in plant–bacteria interactions (Costacurta and Vanderleyden 1995; Bashan and Holguin 1998; Patten and Glick 2002; Molina-Favero et al. 2008). IAA acts as a signaling molecule in microorganisms including bacteria (Bianco et al. 2006; Liu and Nester 2006; Yang et al. 2007; Yuan et al. 2008; Spaepen et al. 2009) because it affects gene expression in some microorganisms. Extensive communication occurs between plants and bacteria during different stages of plant development in which signaling molecules from the two partners play an important role. Bacteria are capable to detect the plant host and initiate their colonization strategies in the rhizosphere by producing growth-regulating substances such as IAA. On the other hand, plants are able to recognize microbe-derived compounds and adjust their defense and growth responses according to the type of microorganism encountered. This molecular dialog will determine the final outcome of the relationship, ranging from pathogenesis to symbiosis, usually through highly coordinated cellular processes (Bais et al. 2004). IAA like quorum sensing molecules may play a role in plant–bacterial signaling (Loper and Schroth 1986; Idris et al. 2007; Phi et al. 2008; Van Puyvelde et al. 2011). For example, IAA triggers a broad gene expression response in *Azospirillum brasilense* (Van Puyvelde et al. 2011) and IAA synthesis is controlled by a positive feedback transcriptional mechanism (Vande Broek et al. 1999). In addition to the hypothesis that bacterial IAA contributes to evade the host defense by derepressing the IAA signaling in the plant, IAA also have a direct effect on bacterial survival and its resistance to plant defense (Remans et al. 2006). Evidence has been accumulating that some microorganisms, independent of their ability to produce IAA, make use of IAA as a signaling

molecule steering microbial behavior. These results led to the speculation that signaling by indole may have a role in adaptation of bacterial cells to a nutrient-poor environment where amino acid catabolism is an important energy source (Wang et al. 2001). Other targets of indole mediated signaling were found signifying a role for indole signaling in biofilm formation (Domka et al. 2006). Other evidence has accumulated indicating that classic plant signals such as IAA can be produced by microorganisms to efficiently colonize the root and control root system architecture (Randy et al. 2009). Many studies have shown that bacterial IAA is known as an effector's molecule in plant–bacteria interactions, both in pathogenesis and phytostimulation. It has been shown that bacterial IAA biosynthesis contributes to colonization capacity and fitness on the host. A low IAA-producing mutant of *P. fluorescens* HP72 is reduced in colonization ability on bent grass roots as compared with the wild-type (Suzuki et al. 2003). It is logical to postulate that bacteria use IAA as part of their colonization strategy by stimulating proliferation of plant tissues and thus enhanced colonization surface and exudation of nutrients for bacterial growth. Some similarity exists between IAA signaling in bacteria–plant interactions, in which IAA is produced by both partners, and signaling by bacterial quorum sensing molecules in bacteria–host interactions (Spaepen et al. 2007). However, the ecological significance of IAA production by bacteria would be more conclusive if it could be established that bacterial IAA production occurs while bacteria colonize the root system. As both the plant and the bacteria synthesize and secrete IAA, it is difficult to address the contribution of one particular hormone responsible for the effects observed (Spaepen et al. 2007). Nevertheless, it seems bacterial IAA, together with endogenous plant-synthesized IAA may have significantly affected plants and bacterial colonization as mentioned above (Fig. 2).

7 Bacterial IAA in Endophytic and Rhizosphere Colonization

The IAA-producing PGPRs can stimulate root growth and seed germination, modify the architecture of the root system, enhance root exudates and eventually increase the root biomass. These bacteria can facilitate more colonization of endophytic and rhizosphere PGPRs. Enhanced root system and exudates in turn have many other effects as shown in Table 1.

7.1 IAA in Endophytic Bacterial Colonization

Endophytic bacteria can be defined as those bacteria that colonize the internal tissue of the plant showing no external sign of infection or negative effect on their host (Ryan et al. 2008). These bacteria significantly affect plant growth by different mechanisms, which is similar to those used by associative bacteria

Table 1 Effects of resulting from increasing root exudates and root system by IAA-producing PGPRs

Increasing root exudates	Increasing root system
• Affecting growth and metabolism of biocontrol agents	• Enhancing the plant access to nutrients
• Altering the diversity and activity of plant-associated microbes	• Increasing plant growth
• Serving as important nutrients, attractants and deterrents	• Increasing root exudates
• Mobilizing nutrients (toxic/essential ions) such as phosphorus and micronutrient and/or metal immobilization	
• Complexation of toxic and essential ions and increase their mobility for plant uptake	
• A major driving force for microbial root colonization	
• Prolonging metabolic activity	
• Extending colonization persistence	
• Influencing on overall biological control performance	
• Effecting on the physical and chemical properties of the soil and on the indigenous microflora	
• Uptake of nutrient ions by the plant	
• Supporting higher populations of microflora	

(Lugtenberg and Kamilova 2009). Numerous endophytes are actively involved in the synthesis of IAA in pure culture and in plants and increased root growth and root length, resulting in greater root surface area that enables the plant to access more nutrients from soil (Jacobson et al. 1994; Boiero et al. 2007). Production of pectinase and cellulase (pectinolytic activity) are common features of endophytic bacteria (Elbeltagy et al. 2000) responsible for plant invasion by them (Teaumroong et al. 2001). Endophytic bacteria may colonize root tissues and spread actively in aerial parts of plants through expressing moderate amount of degradative enzymes (pectinases and cellulases) (Adriano-Anaya et al. 2006). Utilization of previously mentioned enzymatic activities for colonization by PGPRs has been revealed as one of the efficient methods to get entry into the host plant. Endoglucanase is one of the major determinants for the colonization of endorhizosphere, which was evident from the observation that *Azoarcus* strain lacking endoglucanse was not effective in colonizing the rice plants. The endoglucanase loosens larger cellulose fibers, which may help entering into the plant. However, in our studies, most of the root and rhizosphere isolates produced pectinases and cellulases and some of the isolates were not positive for activity of cellulases and pectinases (Etesami et al. 2014b). In addition, genes encoding plant cell wall degrading enzymes have not been found in endophytic bacteria *Herbaspirillum seropedicae* strain SmR1 (Pedrosa et al. 2011). Previous studies that have shown invasion can happen through lesions particularly occurring on the lateral or adventitious roots. This is through root hairs and between undamaged epidermal cells fissures at the lateral root base and by cortical, intercellular crack

entry (Chaintreuil et al. 2000; Sevilla et al. 2001; James et al. 2002). Chi et al. (2005) demonstrated that the colonization of *gfp*-tagged rhizobia in crop plants begins with surface colonization of the rhizoplane at lateral root emergence, followed by endophytic colonization within roots and then ascending endophytic migration into the stem base, leaf sheath and leaves where they develop high populations. *Azospirillum* may also colonize endophytically through wounds and cracks of the plant root (Reinhold-Hurek and Hurek 2011). The colonization of the interior of plant roots by microbial endophytes appears as a most attractive goal, because their plant nutrient resources can be explored even more effectively without the tough competition with the high number of other microbes colonizing the root surface and environment (Rosenblueth and Martinez-Romero 2006; Schulz et al. 2006). However, in this case, the efficient interaction with the plant host gets even more important. The success of invasion and survival within the host also requires that bacteria overcome plant defense responses prompted after microbial recognition, a process in which surface polysaccharides, antioxidant systems, ethylene biosynthesis inhibitors and virulence genes are involved (Soto et al. 2006). However, it can be speculated that IAA production trait is part of the strategy used by IAA synthesizing bacteria to bypass the plant defense system. It has been observed previously that IAA interfere with parts of the host defense system. IAA is able to block several pathogenesis-related (PR) enzymes, including β-glucanase (Mohnen et al. 1985; Jouanneau et al. 1991; Lim and Kim 1995) and chitinase (Shinshi et al. 1987) at the mRNA level. The link between plant defense and IAA signaling gives an extra dimension to the role of bacterial IAA in colonization ability (Spaepen et al. 2007). The capacity to synthesize IAA is common among endophytic bacteria. Most of endophytic diazotroph isolates (62.75 %) in the study conducted by Teaumroong et al. (2001) also produced a significant amount of IAA. Endophytic bacterial isolates from *Thai* rice also showed a high N_2-fixation potential and were able to produce PGP substances such as IAA (Teaumroong et al. 2001). This suggests that the ability of IAA production may help IAA-producing or IAA-non-producing bacteria (with and without pectinolytic activity) invade inside plant roots. In such a process, IAA which is a plant hormone with no apparent function in bacterial cells could improve the fitness of the plant–bacterium interaction. Brandl and Lindow (1998) have studied the contribution of IAA for bacterial epiphytic fitness, and their observations were supported by the investigations of other workers (Glick 1995; Dobbelaere et al. 1999; Verma et al. 2001). Since the first step of bacteria invasion in plant root comprises of the attachment of isolates onto epidermal cells of the root surface, where root hair zone shows one of the major sites of primary colonization (mainly on the basal region of emerging hairs), it is possible that IAA-producing bacteria by increased root system can colonize plant roots better than other bacteria (Katherine et al. 2008; Prieto et al. 2011). In addition, IAA levels weaken plant defense mechanisms making colonization easier. Bacterial IAA can loosen plant cell walls and as a result promotes an increase in root exudation that provides additional nutrients to support the growth of rhizosphere bacteria (James et al. 2002; Chi et al. 2005). Since endophytic microbial communities originate from

the soil and rhizosphere (Hallmann 1997; Sturz et al. 2000; Elvira-Recuenco and Van Vuurde 2000), bacterial IAA can attract more rhizosphere bacteria by increasing root exudation. Bacterial IAA stimulates the development of the root system of the host plant (De Salamone et al. 2005) and IAA-producing isolates can improve the fitness of plant–microbe interactions (Brandl and Lindow 1998; De Salamone et al. 2005). Mendes et al. (2007) showed most of the IAA-producing isolates were found among the stem endophytes, followed by root endophytes and rhizosphere isolates. Previous studies indicate higher frequency of IAA-producing bacteria in root compared to rhizosphere (Kuklinsky-Sobral et al. 2004; Mendes et al. 2007; Etesami et al. 2014b). The observation that the frequency of IAA-producing bacteria is higher in the roots than in the rhizosphere of plants suggests that plants select for endophytic bacteria with this trait or that IAA-producing bacteria harbor other traits that allow them to more effectively reach and establish themselves in the inner plant tissue (Mendes et al. 2007). IAA of microbial origin in the interior of plants could induce a physiological response in the host plant. Therefore, screening of the endophytes for their in vitro potential of IAA production could provide a reliable base for selection of effective PGP bacteria (Patten and Glick 2002; Etesami et al. 2015). In general, IAA-producing bacteria by increasing root system and root exudates can have effective role in colonization themselves or other bacteria inside or on plants, explained separately in the following sections.

7.1.1 IAA and Root Exudates

One of the main effects of bacterial IAA is the enhancement of lateral and adventitious rooting leading to improved nutrient uptake and root exudation that in turn stimulates bacterial proliferation on the roots (Tien et al. 1979; Fallik et al. 1988; Xie et al. 1996; Okon and Vanderleyden 1997; Dobbelaere et al. 1999; Lambrecht et al. 2000; Steenhoudt and Vanderleyden 2000; Himanen et al. 2002; Tsavkelova et al. 2007). Rhizosphere and rhizoplane colonization and after that endophytic colonization has been described to be linked to root exudation (Lugtenberg and Dekkers 1999). Carbon fixed by plant photosynthesis is known to be partly translocated into the root zone and released as root exudates (Bais et al. 2006). Various carbohydrates, amino acids (L-Trp), organic acids, as well as other compounds, which provide a source of nutrients for root-associated bacteria, are released in the rhizosphere (Jones 1998; Walker et al. 2003). Microorganisms are known to be chemoattracted and move toward exudates, allowing them to colonize and multiply both in the rhizosphere and in the rhizoplane (Lugtenberg and Kamilova 2009). It is known that bacterial IAA can loosen plant cell walls and as a result promotes an increasing amount of root exudation that provides additional nutrients to support the growth of rhizosphere bacteria (James et al. 2002; Chi et al. 2005). Many compounds present in the root exudates stimulate a positive chemotactic response in bacteria (Somers et al. 2004; Kumar et al. 2007a). Being a major driving force for microbial root colonization, plant root exudation

could stimulate microbial colonization on the roots. In addition, greater exudation or nutrient availability may prolong metabolic activity, extend colonization persistence and enhance expression of certain traits (Pielach et al. 2008). Overall, bacterial IAA increases root surface area and length and thereby provides the plant with greater access to soil nutrients. In addition, IAA stimulates overproduction of root hairs and lateral roots in plants and release of saccharides from plant cell walls during the elongation (Davies 2004). Saccharides are a source of nutrients for microorganisms and can increase the colonization ability of plant-associated bacteria (Lindow and Brandl 2003). Failure of PGPRs to produce a desired effect after seeds inoculation is frequently associated with their failure to colonize plant roots (Benizri et al. 2001). The host plants may provide a satisfactory environment for bacteria to proliferate and produce excessive amounts of IAA, thus weakening the plant and promoting root colonization. Since bacterial attachment to plant surfaces begins with attraction by seedling root exudates (Begonia and Kremer 1994; Bellis and Ercolani 2001), bacterial IAA can increase colonization by loosening plant cell walls and as a result facilitating an increasing amount of root exudation. IAA may also regulate root exudation through changing plasmalemma permeability (Brandl and Lindow 1998). It was hypothesized that the production of rhizobacterial IAA contributes to circumvent the plant defense system by depressing auxin signaling (Spaepen et al. 2007). The expression of IAA biosynthesis genes in bacteria colonizing the plant root zone testifies to the importance of IAA production for this colonization (Rothballer et al. 2005). As reviewed by Spaepen et al. (2007), regardless of their ability to produce IAA, bacteria can use the phytohormone as a signaling molecule to trigger the expression of genes related to survival under stress. Therefore, IAA can be involved both in the establishment of plant–bacteria associations and in the regulation of their functioning under changing environmental conditions. Since endophytic microbial communities originate from the soil and rhizosphere (Hallmann 1997; Sturz et al. 2000; Elvira-Recuenco and Van Vuurde 2000), bacterial IAA can attract more rhizosphere bacteria and as a result endophytic bacteria by increasing more amount of root exudation. As the amount of photosynthates secreted as root exudates varies with the type of soil and the availability of nutrients (Kraffczyk et al. 1984; Paterson and Sim 2000), the effect of bacterial IAA in the amount of root exudation and subsequently root colonization can also be different under changing conditions.

7.1.2 IAA and Root System

Bacterial IAA plays a major role in promotion of root elongation when a bacterium is associated with its host plant (Dangar and Basu 1987; Lynch 1990; Arshad and Frankenberger 1991; Glick 1995; García de Salamone et al. 2001; Gutiérrez-Mañero et al. 2001; Persello-Cartieaux et al. 2003; Dobbelaere et al. 2003; Vivas et al. 2005). Promotion of root growth is one of the major markers by which the beneficial effect of PGPRs is measured (Glick 1995). Almost all endophytic bacteria were also found in the rhizosphere, thus supporting the hypothesis that there

is a continuum of root-associated bacteria from the rhizosphere to rhizoplane to epidermis and cortex (Kloepper and Beauchamp 1992; Quadt-Hallman et al. 1997). This might explain the close relationship between endophytic and rhizosphere colonizing bacteria. Except for bacteria transmitted through seeds, potential endophytes must first colonize the root surface prior to entering the plant. Potential internal colonists find their host by chemotaxis, electrotaxis, or accidental encounter. Lipopolysaccharides, flagella, pili and twitching motility (Dörr et al. 1998; Böhm et al. 2007) have been shown to affect endophytic colonization and bacterial mobility within host plants. Motility of beneficial associative PGPRs has been described for several bacteria such as *Alcaligenes faecalis*, *A. brasilense* and *P. fluorescens* (Bashan 1986; You et al. 1995). In addition, the secretion of cell wall degrading enzymes is involved in bacterial penetration (Lodewyckx et al. 2002) and spreading within the plant. The penetration process does not necessarily involve active mechanisms and thus all rhizosphere bacteria can be expected to be endophytic at one stage of their life (Hardoim et al. 2008). Entry into a plant tissue can also be via the stomata, lenticels, wounds (including broken trichomes), areas of emergence of lateral roots and emerging radicles. However, the main entry for endophytic bacteria appears to be through wounds that naturally occur because of plant growth or through root hairs and at epidermal conjunctions (Reinhold-Hurek and Hurek 1998). Several authors have reported extensive colonization of the secondary root emergence zone (site of root branches) by bacterial endophytes (Hallmann 1997). The fact that colonization is especially abundant in root tissue may reflect the fact that the root is the primary site where endophytes gain entry into plants. A criterion for some endophytes to colonize the plant is thus must find their way through cracks formed at the emergence of lateral roots or at the zone of elongation and differentiation of the root. During the colonization process, migration of bacteria toward roots is dependent on active motility of bacteria and passive movement of bacteria in percolating water, on vectors, or via carrying and deposition by elongating root tips (Parke 1991; Walker et al. 2002; Bowen and Rovira 1991). Percolating water may enhance root colonization due to the transport and spread of bacteria. Root elongation and expansion can also be involved in transporting bacteria down the root. IAA together with ACC deaminase activity can help transport bacteria by increasing root elongation. In addition, there are many independent evidences using microbiological and molecular techniques indicating that roots stimulate soil microbial communities selectively creating unique rhizosphere communities (Duineveld et al. 1998; Marschner et al. 2001; Rengel and Marschner 2005). IAA by increasing root system may help this selection. In view of function of bacterial IAA in increased root system, it is proposed that IAA-producing bacteria can provide more number of active sites and access to colonization for other PGPRs. For example, the presence of PGPRs in the root vicinity could improve ability of rhizobia to compete with indigenous populations for nodulation. Parmar and Dadarwal (2000) reported that increase in root growth provides more number of active sites and access to nodulation for rhizobia in chickpea.

7.2 IAA in Epiphytic Bacterial Colonization

The biosynthesis of IAA is widespread among bacterial colonizers of the phyllosphere (Fett et al. 1987; Glickmann et al. 1998; Lindow et al. 1998; Brandl et al. 2001). Because IAA is involved in many aspects of plant development, it is of great importance that bacteria which colonize plant surfaces have the ability to synthesize an IAA matching that found in plants. Many studies reported the contribution of IAA for bacterial epiphytic fitness (Glick 1995; Patten and Glick 1996; Bastián et al. 1998; Brandl and Lindow 1998; Dobbelaere et al. 1999; Verma et al. 2001). It is hypothesized that the secretion of IAA may modify the microhabitat of epiphytic bacteria by increasing nutrient leakage from plant cells; enhanced nutrient availability may better enable IAA-producing bacteria to colonize the phyllosphere and may contribute to their epiphytic fitness (Brandl et al. 1996). In competition experiments, an IAA-producing strain of *Pantoea agglomerans* reached twice the population size of an isogenic IAA-deficient mutant on pear flowers in the field and on bean plants in the greenhouse (Brandl and Lindow 1998). This increase in the ratio of the population size of the parental strain over that of the IAA-deficient mutant occurred only during periods of active colonization of the plants. IAA production in *P. agglomerans* was also associated with increased fitness during periods of drought stress on plants (Manulis et al. 1998). IAA stimulates the release of saccharides from the plant cell wall (Goldberg 1980; Vanderhoff and Dute 1981; Fry 1989). Because bacteria on plants are frequently nutrient limited (the nutrient concentration including glucose and other sugars on leaves ranges from 3 to 20 mg L^{-1}) (Chet et al. 1973; Fokkema and Lorbeer 1974), it is hypothesized that the greater epiphytic fitness of IAA-producing strains resulted from enhanced nutrient availability caused by increased leakage of saccharides from plant cells in their vicinity. Brandl et al. (1996) showed a similar release of nutrients from plant cells in response to IAA produced by epiphytic bacteria on plants, which convene upon a selective advantage. Brandl and Lindow (1998) conducted the epiphytic fitness of strains *Erwinia herbicola* 299R and 299XYLE, an isogenic IAA-deficient mutant of strain 299R, evaluated in greenhouse and field studies by analysis of changes in the ratio of the population sizes of these two strains after inoculation as mixtures onto plants. Populations of the parental strain increased to approximately twice those of the IAA-deficient mutant strain after co-inoculation in a proportion of 1:1 onto bean plants in the greenhouse and onto pear flowers in field studies. They showed that IAA synthesis could contribute to the growth of strain 299R on plant surfaces. Their results clearly indicate that a benefit of IAA production occurs primarily when cells can exploit resources in the phyllosphere for further growth. Work performed with the non-pathogenic *E. herbicola* 299R strain showed that *ipd*C transcription increased 32-fold *in planta* on leaves of bean and tobacco and 1000-fold on pears flowers (Brandl and Lindow 1997). Studies involving with wild-type and *ipd*C mutant have demonstrated that IAA production contributed to epiphytic fitness of the bacteria on bean plants and pear

blossoms, because the *ipd*C mutants exhibited a tenfold reduced fitness when compared to wild-type strain (Brandl and Lindow 1998). This change in the proportion of IAA-producing to IAA-deficient strains in mixed populations on leaves appears also to reflect a plant specific benefit of IAA production, since no difference in the growth of these two strains was noted in culture. They concluded that this benefit may be mediated by the increased leakage of nutrients from plant cells in the vicinity of IAA-producing bacteria colonizing the plant surface. Another example is *E. herbicola*, a common colonist on plant surfaces such as leaves and buds. *E. herbicola* produces IAA through L-Trp-independent pathways. IAA can increase colonization of plant surfaces by this epiphyte (Brandl and Lindow 1996; Lindow and Brandl 2003). Earlier, Varvaro and Martella (1993) have shown that IAA-deficient mutants of *Pseudomonas syringae* pv. *savastanoi*, obtained by selection for resistance to α-methyltryptophan, reduced in their ability to colonize and survive on olive leaf surfaces. They also tested the importance of IAA production in bacterial colonization of bean leaves with the brown spot pathogen *P. syringae* pv. *syringae* and an IAA-deficient mutant derived by insertional mutagenesis (Mazzola and White 1994). Their results showed IAA biosynthesis is not essential for bacterial growth and survival, since IAA-deficient mutants as well as their IAA-producing parental strain grew in vitro (Brandl and Lindow 1996; Smidt and Kosuge 1978). Increased transcriptional activity of *ipd*C during the growth of *E. herbicola* 299R on plant surfaces provides some evidence for the bacterial production of IAA in the phyllosphere (Brandl and Lindow 1997, 1998). Their results thus indicate that bacterial IAA synthesis can affect the normal physiology of plant cells. Exogenously applied IAA can stimulate the release of large quantities of monosaccharides and oligosaccharides from the plant cell wall (Fry 1989; Goldberg 1980). Therefore, IAA-producing bacteria may modify their microhabitat or the microhabitat of other bacteria by increasing nutrient leakage from plant cells; enhanced nutrient availability may better enable them to colonize the phyllosphere and may contribute to their epiphytic fitness.

8 IAA and Solubilization of Phosphorous

After nitrogen, the essential mineral element that most frequently limits the growth of plants is phosphorus (P), which only is taken up in monobasic ($H_2PO_4^-$) or dibasic (HPO_4^{2-}) soluble forms (Glass 1989). Although soils generally contain a large amount of total P but only a small fraction is available for plant uptake (Khan et al. 2006). Substantial amounts of phosphate fertilizers are applied to agricultural soils due to relative immobility of phosphate and its very low concentration in soil solutions. This results in an accumulation of large quantities of total phosphorus in the soil, of which 20–80 % is in organic form (Richardson 1994). However, plants are well adapted to uptake of P from low

concentration soil solution (Jungk 2001). Therefore, it is presumed that the supply and availability of P to the root surface is influenced by the root and microbial processes. The plant-associated microorganisms improve the plant nutrient acquisition by mobilizing nutrients and making it available to plant roots. An example is the P-solubilizing bacteria, which dissolves various sparingly soluble P sources such as $Ca_3(PO_4)_2$ (Rodriguez et al. 2004) and $Zn_3(PO_4)_2$ (Saravanan et al. 2007) through lowering pH of the rhizosphere soil and making P available for plant uptake. The increased plant growth and P uptake have been reported on the inoculations of P-solubilizing *Pseudomonas* sp. in wheat (Babana and Antoun 2006), *Pantoea* J49 in peanut (Taurian et al. 2010) and *Psychrobacter* sp. SRS8 in *Ricinus communis* and *Helianthus annuus* (Ma et al. 2010). Furthermore, presence of high levels of heavy metals in soil interferes with P uptake and lead to plant growth retardation (Zaidi et al. 2006). Under metal stressed conditions, most metal-resistant PGPRs (specially ACC deaminase-producing bacteria) can either convert these insoluble phosphates into available forms through acidification, chelation, exchange reactions and release of organic acids (Chung et al. 2005) or mineralize organic phosphates by secreting extracellular phosphatases (Gyaneshwar et al. 2002; van der Heijden et al. 2008). As mentioned above, PGPRs stimulate the plant growth directly through increase in nutrition acquisition, such as phosphate solubilization, or more generally by rendering the inaccessible nutrients available to the plants (Persello-Cartieaux et al. 2003). Bacterial IAA can increase the root exudates and root system through soil pH and nutrient status. Exudation of organic acids from root results in acidification of the rhizosphere (Amir and Pineau 2003; Dakora and Philips 2002; Jones et al. 2003). The organic acids play an important role in the complexation of toxic and essential ions and increase their mobility for plant uptake. An acidic pH is typical for the rhizosphere environment due to proton extrusion through membranes of root cells (Spaepen et al. 2007). The acidification can also contribute to plant growth by mobilizing nutrients such as phosphorus and micronutrient. Acidification of the surrounding soil can occur with the release of protons and organic acids from the seed and root and uptake of nutrient ions by the plant (Hartman et al. 2009). In addition, phosphorous deficiency in many plants enhances the production and release of phenolic and carboxylate compounds (Hartman et al. 2009). Altered root morphology of inoculated plants may enhance phosphorus uptake. Furthermore, root hair abundance and length are also positively correlated with increased uptake of relatively immobile elements such as phosphorus. Datta et al. (1982) reported that a P-solubilizing and IAA-producing strain of *Bacillus firmus* increased the grain yield and P uptake of rice in a P-deficient soil amended with rock phosphate. In general, in view of function of bacterial IAA in increasing root exudates and root surface area (Dobbelaere et al. 1999; Lambrecht et al. 2000; Steenhoudt and Vanderleyden 2000) (Fig. 2), it may be suggested that IAA-producing bacteria can also solubilize insoluble phosphates similar to phosphate-solubilizing bacteria (Fig. 3).

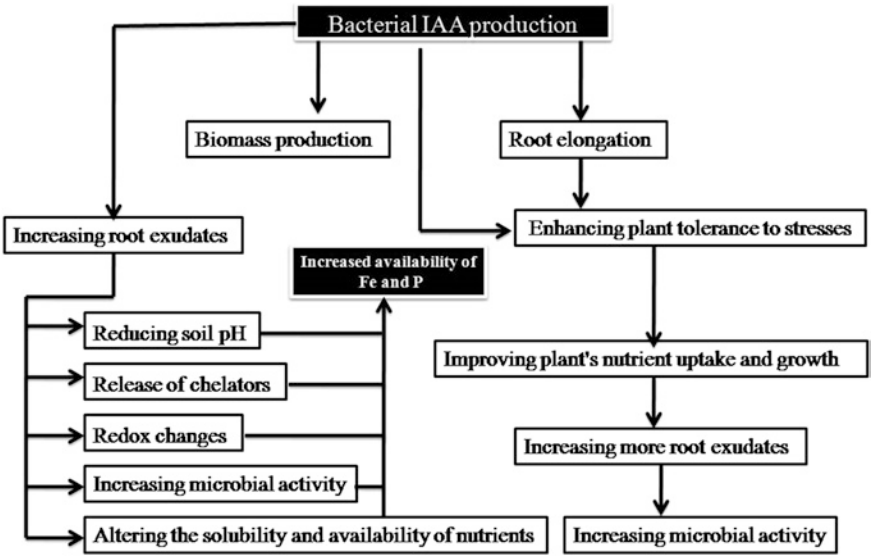

Fig. 3 Functions of bacterial IAA in obviating some of the roles of siderophore-producing bacteria and phosphate-solubilizing bacteria

9 IAA and Availability of Iron

Iron is a necessary cofactor for many enzymatic reactions. Under aerobic conditions, iron exists predominantly as Fe^{3+} and reacts to form highly insoluble hydroxides and oxyhydroxides that are basically unavailable to plants and microorganisms. High soil pH reduces while acidic soil conditions increase Fe availability. As pH increases by one unit, activity of Fe^{3+} decreases by 1000-fold. Under reducing conditions, addition of H^+ or other reductants, Fe solubility increases. Under such situations, Fe can be adsorbed on soil as an exchangeable ion. To acquire sufficient iron, plants under iron stress release phytosiderophores or protons and chelators (phenolics, carboxylates) to acquire iron (Hartman et al. 2009). Poorly soluble inorganic nutrients can be made available through the secretion of organic acids. Most plant-associated bacteria can produce iron chelators called siderophores in response to low iron levels in the rhizosphere. Several examples of increased Fe uptake in plants with concurrent stimulation of plant growth as a result of PGPRs inoculations have been reported (Burd et al. 2000; Carrillo-Castañeda et al. 2003; Barzanti et al. 2007). Exudation of organic acids from root has resulted in acidification of the rhizosphere (Dakora and Philips 2002). Acidification of rhizosphere through organic acids can contribute to plant growth by mobilizing nutrients such as P and Fe. In addition, organic acids are capable of chelating Fe^{3+} and making it available to plant roots. Some of the compounds in root exudates are able to form Fe complexes that improve

availability. Carbohydrates, amino acids, organic acids, phenolics and secondary metabolites (low-molecular-weight compounds), proteins and mucilage (high-molecular-weight components) are typically the dominant soluble reduced carbon compounds in rhizodeposits (Lynch and Whipps 1990; Farrar et al. 2003; Wen et al. 2007; Badri and Vivanco 2009). Because of function of IAA in secreting root exudates and increasing rooting system and, since these exudates are involved in acidifying rhizosphere and in providing a reducing conditions required for converting Fe^{3+} to Fe^{2+}, it may be suggested IAA-producing bacteria can also solubilize insoluble Fe sources and induce plant growth and iron uptake in a similar manner to siderophore-producing bacteria (Fig. 3). For example, protons and electrons are secreted within carbon compounds as undissociated acids or compounds with reducing capabilities. Oxygen consumption, due to respiration by the root (increase of root system due to bacterial IAA) and associated microflora (increase of microflora activity due to production of more root exudates), can also result in steep redox gradients in the rhizosphere (Hartman et al. 2009). Because in the aerobic environment, iron occurs principally as Fe^{3+} and is likely to form insoluble hydroxides and oxyhydroxides, thus it is generally inaccessible to both plants and microorganisms (Rajkumar et al. 2010).

10 IAA in Phytopathogenesis

Production of IAA is common among plant-associated bacteria, which may be beneficial or detrimental to the plant health. For example, IAA production by *P. putida* GR12-2 has been found to improve the root proliferation resulting in increased root surface area, which helps in rise of nutrient and water uptake from soil (Patten and Glick 2002). On the other hand, in some reports, IAA production has been found necessary for pathogenesis (Vandeputte et al. 2005; Yang et al. 2007). Plant–microbe interactions were determined by different IAA biosynthesis pathways. For instance, the beneficial plant-associated bacteria synthesize IAA via the indole-3-pyruvate (IPyA) pathway, whereas pathogenic bacteria mainly use the indole-3-acetamide (IAM) pathway (Patten and Glick 1996, 2002; Manulis et al. 1998; Hardoim et al. 2008). For example, in phytopathogenic bacteria, such as *Agrobacterium tumefaciens* and pathovars of *P. syringae*, IAA is synthesized from L-Trp via the intermediate IAM pathway and has been connected to the induction of plant tumors (Glickmann et al. 1998; Patten and Glick 2002; Buell et al. 2003). The production of phytohormones such as IAA and cytokinins in free-living cultures is an indication of many phytophatogenic gall forming bacteria such as *P. agglomerans*, *P. savastanoi* pv. *savastanoi*, *P. syringae* pv. *syringae*, *Ralstonia solanacearum* and *Rhodococcus fascians* (Morris 1995; Vandeputte et al. 2005). In many bacterial pathogens, the *hrp*-gene encoded type III secretion system that directly translocates effector proteins into the eukaryotic host cells is fundamental to pathogenesis and the development of disease symptoms (Jin et al. 2003; He et al. 2004). In *P. syringae*, the presence of a functional *Hrp* promoter

upstream of the *iaa*L gene involved in IAA biosynthesis further supports the role for IAA production in virulence (Fouts et al. 2002). The results of Navarro et al. (2006) suggest that decreasing plant IAA signaling can increase resistance to bacterial pathogens. A possible mechanism is the expression of IAA-repressed plant defense genes. They further showed that exogenous application of IAA enhances susceptibility to bacterial pathogens. These findings allow us to hypothesize that bacterial IAA production may contribute to circumvent the host defense system by deactivating repressor gene of IAA signaling. In this way, IAA biosynthesis may play an important role in bacterial resistance and colonization on the plant (Remans et al. 2006). For disease development, the first step is to infect the plant host and obtain nutrients to support the pathogen's growth and survival. In *E. herbicola*, the presence of IAA increases the ability of the bacterium to colonize on plant surfaces (Brandl and Lindow 1996) and the loss of IAA production decreases the colony size and population growth (Lindow and Brandl 2003). For example, a twofold population increase relative to IAA-deficient strains in pear flowers and bean plants was reported in IAA-producing *P. agglomerans* (Brandl and Lindow 1996). It has also been suggested that bacteria synthesize IAA to stimulate the root hairs production and lateral roots in plants relating to release saccharides from plant cell walls during the elongation (Davies 2004). Saccharides are carbohydrates that can be a source of nutrients for microorganisms, increase the colonization ability of a bacterium (Lindow and Brandl 2003) and facilitate bacterial colonization of plant surfaces (Bender et al. 1999). In addition, IAA production has been demonstrated to be a virulence factor in some pathogens (Yamada 1993). Many microorganisms produce IAA in order to perturb host physiological processes for their own benefits (Costacurta and Vanderleyden 1995; Yamada 1993). Exogenous application of IAA produced by pathogens enhances susceptibility to bacterial pathogens. In their interaction with plants, these microorganisms can interfere with plant development by disturbing the IAA balance in plants. This is best documented for phytopathogenic bacteria like *Agrobacterium* spp. and *P. savastanoi* pv. *savastanoi*, causing tumors and galls, respectively (Jameson 2000; Mole et al. 2007), and PGPR such as *Azospirillum* spp. that have impact on plant root development (Persello-Cartieaux et al. 2003; Spaepen et al. 2007). As many bacterial pathogens are known to produce IAA, it can be speculated that this property is part of the strategy used by the pathogen to bypass the plant defense system. The same could apply for IAA-producing PGPRs. Rhizobacteria may affect plant hosts by mechanisms similar to phytopathogenic bacteria through production of enzymes, phytotoxins, or phytohormones (Loper and Schroth 1986; Schippers et al. 1987). Nevertheless, biotrophic phytopathogens and plant-beneficial bacteria are coming closer to each other when taking an IAA perspective. Obviously, as we try to comprehend the challenges in one direction (phytopathology) new and fascinating questions raises in another direction (phytostimulation). In general, the function of bacterial IAA in pathogenesis and disease development is not entirely clear.

11 IAA in Rhizobium–Legume Symbiosis

The IAA produced by PGPRs is involved in plant–bacteria interactions and can affect plant growth promotion and root nodulation. They are involved in many processes of nodule formation by rhizobia in legume plants, such as founder cell specification, nodule initiation and differentiation (IAA accumulation), nodule numbers, vascular bundle formation and cell division and differentiation. These three later events are more necessary for nodule formation. Mutants of the bacterium *Bradyrhizobium elkanii* that had a decreased level of IAA synthesis induced fewer nodules on soybean roots than did the wild-type strain (Fukuhara et al. 1994). Nitrogen fixation capacity in the former nodules was also increased (Camerini et al. 2008). In addition, inoculation of *Medicago truncatula* with IAA-overproducing strain resulted in better plant growth under phosphorus deficiency because of the release of organic acids by the bacterium (Bianco and Defez 2010). In co-inoculation studies with *Azospirillum* and *Rhizobium*, earlier and faster nodulation and higher crop yields were observed (Okon and Itzigsohn 1995; Burdman et al. 1996). However, using an *Azospirillum ipd*C mutant, producing 10 % of IAA produced by the wild-type strain, the increase in nodulation and nitrogen fixation was not observed, showing that bacterial IAA production is important in symbiosis (Remans et al. 2008). An extensive overlap of changes in protein level could be observed in *M. truncatula* in response to IAA treatment and *Sinorhizobium meliloti* inoculation, probably because of regulation of these proteins by IAA during the early stages of nodulation (van Noorden et al. 2007). It was demonstrated that the *nod* inducers, the flavonoids, also stimulate the production of IAA by *Rhizobium* (Prinsen et al. 1991). In fact, *A. brasilense* caused a significant increase in the *nod*-inducing activity of crude alfalfa root exudates. IAA could be important for maintaining a functional root nodule (Badenochjones et al. 1983). However, the origin of IAA in the nodules is still not clear. It has been suggested that elevated levels of IAA in nodules are derived from the prokaryotic microsymbiont because a mutant of *Bradyrhizobium japonicum* that produces 30-fold more IAA than the wild-type strain has higher nodulation efficiency (Kaneshiro and Kwolek 1985). Bacteroids of plants inoculated with mutant *B. japonicum* strains produce high amounts of IAA in comparison with wild-type bacteroids, suggesting that increased IAA biosynthesis in nodules is of prokaryotic origin. It is therefore likely that IAA transport regulation is part of the process leading to nodule initiation (Hunter 1989; Kaneshiro and Kwolek 1985). In addition, rhizobia can also indirectly influence the IAA homeostasis by interfering with plant IAA transport (Badenochjones et al. 1983; Ghosh and Basu 2006). Many studies indicate that changes in IAA balance in the host plant are a prerequisite for nodule organogenesis (Mathesius et al. 1998). An IAA-producing *S. meliloti* strain showed increased tolerance to several stresses, and *M. truncatula* plants inoculated with this strain have a higher IAA content in nodules and roots and are better resistant to salt stress (Bianco and Defez 2009). The link between Nod factors as symbiotic signaling molecules and rhizobial IAA production

points to a role for IAA in the *Rhizobium*–legume symbiosis (Theunis 2005). Nevertheless, the exact role of IAA in the different stages of Rhizobium–plant symbiosis remains unclear.

12 IAA in Actinorhizal Symbioses Formation

The term actinorhiza refers both to the filamentous bacteria *Frankia*, an actinobacteria, and to the root location of nitrogen-fixing nodules. Actinorhizal symbioses result from the interaction between *Frankia* and plants belonging to eight angiosperm families collectively called actinorhizal plants (Benson and Silvester 1993). This symbiotic interaction results in the formation of a actinorhizal nodule on the root system, where the bacteria are hosted and fix nitrogen (Obertello et al. 2003). Unlike legume nodules, actinorhizal nodules are structurally and developmentally related to lateral roots (Pawlowski and Bisseling 1996). *Frankia* like many soil bacteria has been known to produce auxins since long ago. For instance, IAA and phenylacetic acid (PAA) are found at relatively high concentration (10^{-5}–10^{-6} M) in the supernatant of various *Frankia* strains in pure culture (Wheeler et al. 1979; Hammad et al. 2003). A specific IAA response might occur in infected cells allowing the infection to proceed. The infection threads are encompassed by the plant cell membrane and a new cell wall-like structure composed mainly of pectin derivatives (Lalonde and Knowles 1975). IAA is known to regulate genes involved in cell wall remodeling and pectin biosynthesis and methylation (Lerouxel et al. 2006). Auxin perception in infected plant cells might therefore be necessary to allow the growth of infection threads (Benjamin et al. 2008).

13 IAA in the Development of Arbuscular Mycorrhizal Symbioses

Arbuscular mycorrhiza (AM), a symbiosis between plants and members of an ancient phylum of fungi, the *Glomeromycota*, improves the supply of water and nutrients, such as phosphate and nitrogen, to the host plant. In return, up to 20 % of plant-fixed carbon is transferred to the fungus. Nutrient transport occurs through symbiotic structures inside plant root cells known as arbuscules. The complex relationship between host roots and AM fungi requires a continuous exchange of signals, which results in the proper development of the symbiosis (Gianinazzi-Pearson 1996; Hause and Fester 2005). Plant hormones are signal molecules known to regulate many developmental processes in plants and are therefore suitable candidates to function in the colonization process and likely during the establishment of an AM symbiosis (Barker and Tagu 2000; Ludwig-Muller and Güther 2007). IAA may facilitate the colonization of a host by increasing the number of

lateral roots as preferential colonization sites for the fungi during early growth phases (Kaldorf and Ludwig-Muller 2000). It is suggested that increased IAA levels and subsequent IAA-induced gene expression might contribute to the phenotypical changes during mycorrhizal colonization (Ludwig-Muller and Güther 2007). Although reports on IAA levels during AM in different plant species are contradictory, the contribution of IAA to the establishment of an AM symbiosis might be an important factor especially for the development of lateral roots which are the preferred infection sites for the fungi (Ludwig-Muller and Güther 2007). Recent findings about the role of fungal-produced IAA in different plant–fungus interacting systems open the possibility that fungi may use IAA and related compounds to interact with plants as part of its colonization strategy, leading to plant growth stimulation and modification of basal plant defense mechanisms (Prusty et al. 2004; Contreras-Cornejo et al. 2009). In maize/*Zea mays* and *A. thaliana*, *Trichoderma* inoculation affected root system architecture, which was related to increased yield of plants. Reported developmental effects include increased lateral root formation and root hair growth (Bjorkman et al. 1998; Harman et al. 2004; Contreras-Cornejo et al. 2009). Studies also indicate that the effects of inoculation with IAA-producing fungi in plants under natural conditions may depend on the type and concentration of IAA produced by the fungi. In general, the increased IAA levels lead to the formation of more lateral roots, which constitute preferential penetration sites for the AM hyphae, thus closing the infection cycle. Future research has to provide functional proof for these hypotheses.

14 IAA and Environmental Stresses

Studies have shown that IAA triggers an increased level of protection against external adverse conditions by coordinately enhancing different cellular defense systems (Lindberg et al. 1985; Frankenberger and Arshad 1995; Bianco et al. 2006; Bianco and Defez 2009). These authors investigated the effect of IAA treatment on bacterial cells and demonstrated that the cells were tolerant to a variety of stress conditions. The role of IAA produced by PGPRs in the promotion of plant growth during stress conditions such as salinity or drought has also been demonstrated (Bianco and Defez 2009; Egamberdieva and Kucharova 2009). Since, indigenously produced IAA in plants decreases in salt stress conditions, salt tolerant PGPRs may increase plant growth and lengthen the root by supplying IAA synthesized by them. Spaepen et al. (2007) reported the role of IAA in response to stress as evident from its increased production of IAA in *Azospirillum* sp. during carbon limitation and acidic pH. An increased tolerance of *M. truncatula* against salt stress was also observed in plants inoculated by the IAA-overproducing strain *S. meliloti* DR-64 (Bianco and Defez 2009). Plants inoculated with this mutant accumulated a high amount of proline and showed enhanced levels of the antioxidant enzymes superoxide dismutase, peroxidase, glutathione reductase and ascorbate peroxidase compared with plants inoculated with the parental strain. In

general, IAA-producing bacteria may enhance growth of plant in drought conditions by stimulating formation of well-developed root system enough for providing sufficient water from soil.

15 Ethylene

The phytohormone ethylene (C_2H_4), a unique plant growth hormone, is found only in gaseous form and produced endogenously by almost all plants (Babalola 2010). Ethylene can function as an efficient plant growth regulator at very low concentrations as low as 0.05 μL^{-1} (Abeles et al. 1992). This phytohormone is involved in the regulation of numerous physiological processes in plants including modulating the growth and cellular metabolism of plants, disease-resistant biotic/abiotic stress tolerance, plant–microbe partnership and plant nutrient cycle (Ping and Boland 2004; Babalola 2010). However, stress conditions such as flooding, wounding, drought, chilling temperature, exposure to chemicals and pathogen attack may induce the production of ethylene substantially (Gnanamanickam 2006; Babalola 2010). The term stress ethylene is used to describe the acceleration of ethylene biosynthesis associated with environmental and biological stresses (Morgan and Drew 1997). The overproduction of ethylene can cause the inhibition of root elongation, lateral root growth and root hair formation (Mayak et al. 2004; Pierik et al. 2006; Saleem et al. 2007; Belimov et al. 2009).

15.1 Ethylene and the Inhibition of Endophytic Colonization

The increased level of ethylene formed in response to stress conditions can be both the cause of some of the symptoms of stress, and the inducer of defense responses, which help to enhance survival of the plant under adverse conditions. The host plant induces defense mechanisms against pathogens. However, in contrast to the plant response to phytopathogens only few defense responses have been described in plant response to endophytes. These differences can be probably explained by the secretion of different compounds or by the amount of secreted metabolites, which may be very low in the case of endophytes (James et al. 2002). However, it has been reported that plants may show defense reactions controlling endophytic colonization (Iniguez et al. 2005). Some plants are known to use salicylic acid (SA), jasmonic acid (JA) and ethylene as signaling molecules, which control colonization by some endophytes inside the root system (Iniguez et al. 2005; Miché et al. 2006). Ethylene has been known as signal molecule and secondary messenger in the induction of a salicylic acid (SA)-independent plant defense pathway referred to as induced systemic resistance (ISR) in plants, decreasing endophytic colonization (Knoester et al. 1998; Pieterse et al. 1998; Ton et al. 2001, 2002; Wildermuth et al. 2001; Audenaert et al. 2002; Iniguez et al. 2005). In a study,

Iniguez et al. (2005) showed addition of ACC to the growth media significantly reduced endophytic colonization in wild-type *Medicago sativa* by *Klebsiella pneumoniae* 342 and *Salmonella enteric*. These evidences suggest that ethylene can significantly inhibit invasion of bacterial cells into plants.

16 ACC Deaminase-Containing PGPR

PGPRs containing ACC deaminase activity can affect plant growth directly through various ways such as nitrogen fixation, solubilization of phosphorus, and increasing growth by regulating endogenous level of plant hormones or indirectly by increasing the natural resistance of the host against pathogens and other environmental stresses (Glick 2004; Lugtenberg and Kamilova 2009; Spaepen et al. 2009). A particular bacterium may affect plant growth using any one, or more, of these mechanisms. Moreover, a bacterium may provide different benefits at various times during the life cycle of the plant. These bacteria can cleave the plant ethylene precursor ACC, and thereby lower the level of ethylene in a developing or stressed plant (Jacobson et al. 1994; Glick 1995, 1998). Under stress conditions, a sustained high level of ethylene may inhibit root elongation (Jackson 1991). Thus, ACC deaminase-producing PGPRs, when bound to the seed coat of a developing seedling, may act as a mechanism for ensuring that the ethylene level does not become elevated to the point where root growth is impaired. By facilitating the formation of longer roots, these bacteria may enhance the survival of some seedlings, especially during the first few days after the seeds are planted. Similarly, ACC deaminase-containing PGPRs bound to the roots of plants can act as a sink for ACC and protect stressed plants from some of the deleterious effects of stress ethylene (Arshad et al. 2008; Belimov et al. 2009). ACC deaminase has been widely reported in numerous species of PGPRs such as *V. paradoxus*, *Agrobacterium genomovars*, *Azospirillum lipoferum*, *Alcaligenes*, *Bacillus*, *Burkholderia*, *Enterobacter*, *Methylobacterium fujisawaense*, *Pseudomonas*, *R. solanacearum*, *Rhizobium*, *Rhodococcus* and *S. meliloti* (Belimov et al. 2001; Dobbelaere et al. 2003; Blaha et al. 2006; Rasche et al. 2006; Pandey and Maheshwari 2007a; Belimov et al. 2009; Duan et al. 2009; Sharp et al. 2011; Jiang et al. 2012; Chen et al. 2013).

16.1 ACC Deaminase in Promotion of Plant Growth

Stimulation of root elongation and biomass production of different plant species by inoculations with PGPRs having ACC deaminase activity has been repeatedly documented, particularly when the plants were subjected to stressful growth conditions (Hall et al. 1996; Burd et al. 1998; Glick 1998; Belimov et al. 2001, 2005; Madhaiyan et al. 2006; Safronova et al. 2006; Glick et al. 2007; Belimov et al.

2009). *P. putida* UW4 deficient in ACC deaminase activity simultaneously lost the ability to elongate roots in infected canola plants (Li et al. 2000). Inoculation of plants with PGPRs containing ACC deaminase activity may lead to various subsequent physiological changes in plants (Glick et al. 2007; Saleem et al. 2007). Considerable evidences have demonstrated the beneficial role of bacterial ACC deaminase in decreasing stress reactions in plant growth under different stresses, including range of pathogenic agents (Arshad and Frankenberger 2002; Arshad et al. 2007; Saleem et al. 2007), salinity, flooding, drought, toxicity of high concentrations of heavy metals present in pollutant soils (Grichko et al. 2000; Grichko and Glick 2001; Nie et al. 2002; Kausar and Shahzad 2006; Zahir et al. 2007; Gamalero et al. 2009; Nadeem et al. 2009) and the presence of toxic organic compounds (Arshad and Frankenberger 2002; Arshad et al. 2007; Glick et al. 2007). Saleem et al. (2007) reviewed the role of PGPRs containing ACC deaminase activity in stress management in agriculture. Following inoculation of pea with the ACC deaminase containing rhizobacterium *V. paradoxus* 5C-2 obtained from pea increased seed nitrogen concentration in plants grown and enhanced vegetative growth and seed yield in drying soil (Dey et al. 2004; Belimov et al. 2009) that may have been due to enhanced nodulation, since ethylene typically inhibits nodulation (Guinel and Geil 2002), attenuated a drought-induced increase in xylem sap ACC concentration in non-nodulated plants and prevented drought-induced decrease in seed nitrogen content of nodulated plants respectively. In addition, adding the ACC deaminase-containing rhizobacterium *V. paradoxus* 5C-2 to the substrate of well-watered, well-fertilized pea plants increased root and shoot growth by 20 and 15 %, respectively (Jiang et al. 2012). Since bacterial mutants having low ACC deaminase activity (including a transposome mutant of *V. paradoxus* 5C-2) did not stimulate plant growth (Glick et al. 1994; Belimov et al. 2007, 2009) and the growth promotion observed was most probably due to decreased plant production of the growth-inhibitory phytohormone ethylene. In other study, Inoculation of *V. paradoxus* 5C-2 significantly ($P < 0.01$) increased fresh biomass of *A. thaliana* by 34–47 % throughout development (Chen et al. 2013). Furthermore, transposon mutagenesis of microorganisms to downregulate ACC deaminase activity reduced or eliminated their growth-promoting effect, in plant–microbe interactions such as canola–*Enterobacter cloacae* (Li et al. 2000), tomato–*Pseudomonas brassicacearum* (Belimov et al. 2007), pea–*V. paradoxus* (Belimov et al. 2009) and canola–*Trichoderma asperellum* (Viterbo et al. 2010). These findings suggested that ACC deaminase plays a key role in promoting plant growth. In general, inoculation with ACC deaminase-containing bacteria induce longer roots which might be helpful in the uptake of relatively more water from deep soil under drought stress conditions, thus increasing water use efficiency of the plants (Zahir et al. 2007). Many studies showed using ACC deaminase-producing bacteria in association with plants subjected to a wide range of different kinds of biotic and abiotic stresses, in all instances tested, resulted in enhanced plant tolerance to the stresses (Table 2). Thus, use of these microorganisms per se can alleviate stresses in agriculture thus opening a new and emerging application of microorganisms.

Table 2 PGPRs conferring abiotic and biotic stress tolerance in crop plants by ACC deaminase activity

Host plant	Bacterial strain	Type of environmental stress	Bacterial effects on plants	References
Ocimum sanctum	*Achromobacter xylosoxidans* Fd2, *Serratia ureilytica* Bac5, *Herbaspirillum seropedicae* Oci9, *Ochrobactrum rhizosphaerae* Oci13,	Flooding	Increase of foliar nutrient uptake, growth and yield	Barnawal et al. (2012)
Tomato (*Lycopersicon esculentum*)	*Enterobacter cloacae* UW4, *E. cloacae* CAL2, *Pseudomonas putida* ATCC17399	Flooding	Improvement of root and shoot growth	Grichko and Glick (2001)
Pea (*Pisum sativum*)	*Variovorax paradoxus* 5C-2	Drought	Improving growth, yield and water use efficiency and increased nodulation by symbiotic nitrogen-fixing bacteria	Belimov et al. (2009)
Wheat (*Triticum aestivum* L.)	SBW17 and SBW27	Drought	Increased root-shoot length, root-shoot mass and lateral root number	Shakir et al. (2012)
Pea (*P. sativum*)	*V. paradoxus*	Drought	Stimulated root biomass by 20–25 %, whole plant biomass was stimulated also by 25 %	Dodd et al. (2005)
Tomato and Pepper	*A. piechaudii* ARV8	Drought	Enhancing the fresh and dry weights	Mayak et al. (2004)
Tomato	*A. piechaudii*	Salinity	Increasing the fresh and dry weights and water use efficiency (WUE)	Mayak et al. (2004)
Canola (*Brassica napus*)	*P. putida* UW4	Salinity	Improved plant growth	Cheng et al. (2007)
Canola (*B. napus*)	*P. putida* UW4	Salinity	Improved plant growth	Cheng et al. (2012)
Mung bean	*Pseudomonas fluorescens* Mk20, *Rhizobium phaseoli* M6	Salinity	Improving seedling growth and nodulation	Amhad et al. (2011)

(continued)

Table 2 (continued)

Host plant	Bacterial strain	Type of environmental stress	Bacterial effects on plants	References
Cucumber	*P. putida* UW4	Salinity	Promoted plant growth, effects on plant biomass, total root length and total leaf projected area, increased AM fungus *Gigaspora rosea* colonization and arbuscule abundance	Gamalero et al. (2008)
Tomato (*Licopersicon esculentum* Mill)	*Bacillus licheniformis* B2r	Salinity	A significant increase in the germination percentage, germination index, root length and seedling dry weight	Chookietwattana and Maneewan (2012)
Cucumber	*P. putida* UW4	Salinity	Increased plant growth, affected root architecture and improved photosynthetic activity	Gamalero et al. (2010)
Canola (*B. napus* L.)	*P. fluorescens, P. putida*	Salinity	Increased seedling growth and the rate of germinating seeds	Jalili et al. (2009)
Catharanthus roseus	*A. xylosoxidans* AUM54	Salinity	Increased germination percentage, vigor index, plant height, root dry weight, increased the antioxidative enzyme content, ascorbate peroxidase (APX) activity, superoxide dismutase (SOD) activity and catalase (CAT)	Karthikeyan et al. (2012)
Maize	*Pseudomonas syringae* S5, *Enterobacter aerogenes* S14, *P. fluorescens* S20	Salinity	Improved the growth and yield, increased plant height, root length, total biomass, cob mass and grain yield	Nadeem et al. (2007)

(continued)

Table 2 (continued)

Host plant	Bacterial strain	Type of environmental stress	Bacterial effects on plants	References
Wheat (*T. aestivum* L.)	*Hallobacillus* sp. SL3, *Bacillus halodenitrificans* PU62	Salinity	Increased root elongation and dry weight	Ramadoss et al. (2013)
Wheat (*T. aestivum* L.)	*P. putida* (W2), *P. fluorescens* (W17)	salinity	Increased plant height, root length, plant biomass and grain yield	Nadeem et al. (2010)
Tomato	*Pseudomonas mendocina*	Salinity	Increasing content of growth	Sadrnia et al. (2011)
Groundnut (*Arachis hypogea*)	*P. fluorescens* TDK1	Salinity	Improving the plant growth parameters, increased yield	Saravanakumar and Samiyappan (2006)
Canola (*B. napus*)	*Brevibacterium epidermidis* RS15, *Micrococcus yunnanensis* RS222, *Bacillus aryabhattai* RS341	Salinity	Increase in root length, dry weight	Siddikee et al. (2010)
Groundnut	*P. fluorescens*	Salinity	Increased yield	Saravanakumar and Samiyappan (2007)
Red pepper	*Brevibacterium iodinum* RS16, *B. licheniformis* RS656, *Zhihengliuela alba* RS111	Salinity	Significantly increase the growth, increase of nutrient uptakes	Siddikee et al. (2011)
Canola (*B. napus*)	*Pseudomonas asplenii* AC	Organics	Significantly increased root and shoot biomass	Reed and Glick (2005)
Mini carnation	*P. fluorescens* YsS6, *Pseudomonas migulae* 8R6, *P. putida* UW4	Flower wilting	Decreased levels of flower senescence	Ali et al. (2012)
Tomato and Castor bean	*P. putida* UW4	Pathogens	Inhibited tumour development on plant	Hao et al. (2007)
Castor bean	*Agrobacterium tumefaciens* D3	Pathogens	Inhibited tumour development on plant, promoted plant root elongation	Hao et al. (2011)

(continued)

Table 2 (continued)

Host plant	Bacterial strain	Type of environmental stress	Bacterial effects on plants	References
Cucumber potato	*P. fluorescens* CHA0	Pathogens	protected cucumber against *Pythium* damping-off and potato tubers against *Erwinia* soft rot	Wang et al. (2000)
Chamaecytisus proliferus	*P. fluorescens*	Pathogens	Controlling the growth of *Fusarium oxysporum* and *Fusarium proliferatum*	Donate-Correa et al. (2005)
Mimosa pudica	*Burkholderia* sp.	Pathogens	Exhibited antagonistic activity against *Rhizoctonia solani* and *Sclerotinia sclerotiorum*	Pandey et al. (2005)
Tomato (*Solanum lycopersicum*)	*P. putida* UW4, *Burkholderia phytofirmans* PsJN, *Azospirillum brasilense* Cd1843	Pathogens	Reduced the development of tumours on plants	Toklikishvili et al. (2010)
Grapevine (*Vitis vinifera* L.)	*B. phytofirmans* PsJN	Low temperature	Increased grapevine growth and physiological activity at a low temperature	Ait Bakra et al. (2006)
Potato	*Burkholderia phytofrmans* PsJN	Heat stress	Maintaining normal growth	Bensalim et al. (1998)
Canola	*P. putida*	Low temperature	Increased yield	Chang et al. (2007)
P. sativum L.	*Pseudomonas brassicacearum*, *Pseudomonas marginalis*, *Pseudomonas oryzihabitans*, *P. putida*, *Pseudomonas* sp., *Alcaligenes xylosoxidans*, *Alcaligenes* sp., *V. paradoxus*, *Bacillus pumilus*, *Rhodococcus* sp.	Heavy metal	The bacteria were tolerant to Cd^{2+} toxicity and stimulated root elongation of rape seedlings in the presence of 300 μM $CdCl_2$ in the nutrient solution	Belimov et al. (2001)

(continued)

Table 2 (continued)

Host plant	Bacterial strain	Type of environmental stress	Bacterial effects on plants	References
Phragmites australis	*P. asplenii* AC[a]	Heavy metal	Inoculation resulted in normal plant growth under high levels of Cu^{2+} and creosote	Reed et al. (2005)
Lycopersicum esculentum Mill	*Kluyvera ascorbata* SUD165 *K. ascorbata* SUD165/26	Heavy metal	Toxic effects of the heavy metals (Ni^{2+}, Pb^{2+} and Zn^{2+}) were not pronounced in inoculated plants	Burd et al. (2000)
Brassica juncea L.	*P. brassicacearum*, *P. marginalis*, *P. oryzihabitans*, *P. putida*, *Pseudomonas* sp., *A. xylosoxidans*, *Alcaligenes* sp., *V. paradoxus*, *B. pumilus*, *Rhodococcus* sp.	Heavy metal	The bacteria were tolerant to Cd^{2+} toxicity and stimulated root elongation of rape seedlings in the presence of 300 μM $CdCl_2$ in the nutrient solution	Belimov et al. (2001)
B. juncea L.	*V. paradoxus*, *Rhodococcus* sp.	Heavy metal	Plant growth was improved in Cd^{2+} supplemented media in response to inoculation.	Belimov et al. (2005)
B. juncea L.	*K. ascorbata* SUD165, *K. ascorbata* SUD165/26	Heavy metal	Toxic effects of heavy metals (Ni^{2+}, Pb^{2+} and Zn^{2+}) were not pronounced in inoculated plants.	Burd et al. (2000)
B. napus	*K. ascorbata* SUD165	Heavy metal	Plant demonstrated normal growth under high levels of Ni^{2+}, Pb^{2+}, Zn^{2+} and CrO_4^{-2}	Burd et al. (1998)
Indian mustard	*V. paradoxus*, *Rhodoccus* sp., *Flavobacterium* sp.	Heavy metal	Increased root length	Belimov et al. (2005)
Canola	*E. cloacae*	Heavy metal	Increased biomass	Nie et al. (2002)
Indian mustard	*A. xylosoxidans*	Heavy metal	Increased root and shoot length and biomass	Ma et al. (2009)

(continued)

Table 2 (continued)

Host plant	Bacterial strain	Type of environmental stress	Bacterial effects on plants	References
P. sativum	*P. brassicacearum* Am3	Heavy metal	Increased Root and shoot biomass	Safronova et al. (2006)
B. juncea	*Pseudomonas* sp. PsA, *Bacillus* sp. Ba32 (RS)	Heavy metal	Plant growth	Rajkumar et al. (2006)
Rape	*P. fluorescens* G10, *Microbacterium* sp. G16	Heavy metal	Increased in biomass production and total Pb uptake, root elongation	Sheng et al. (2008)
Zea mays	*Burkholderia* sp. J62 (RS)	Heavy metal	Increased root and shoot dry weight	Jiang et al. (2008)
Indian mustard, corn, tomato	*Burkholderia* sp.	Heavy metal	Increased biomass	Jiang et al. (2008)

16.2 ACC Deaminase in Endophytic Bacterial Colonization

Successful colonization of the root surface is considered as a key property of prospective inoculants. PGPRs that produce the enzyme ACC deaminase promote plant growth by sequestering and cleaving plant-produced ACC and thereby lowering the level of ethylene in the plant. In experiments, the colonization of root systems with *P. fluorescens*, *P. putida*, *Bacillus pumilus* and *Serratia marcescens* was protected against foliar diseases (Pieterse et al. 2002). Decreased ethylene levels allow the plant to be more resistant to a wide variety of environmental stresses. It has been suggested that the ability to utilize ACC may contribute to the root-colonization ability of bacterial strains. It has been discovered that some PGPRs possess the enzyme ACC deaminase which can cleave ACC, the immediate precursor of ethylene in plants, to α-ketobutyrate and ammonia. The products of this hydrolysis are used by the ACC-degrading PGPRs as nitrogen and carbon sources, and thereby, lower the level of ethylene in a developing seedling or stressed plant. Treatment of plant seeds or roots with ACC deaminase-containing PGPRs typically reduces ACC and ethylene levels about two- to fourfold (Grichko and Glick 2001a; Mayak et al. 2004a). Under stress conditions, ACC deaminase-producing bacteria are able to utilize ACC, thereby increasing the root surface in contact with soil. Since a dynamic equilibrium of ACC concentration exists between root, rhizosphere and bacterium, bacterial uptake of rhizospheric ACC stimulates plant ACC efflux, decreases root ACC concentration and root ethylene evolution, and can increase root growth (Glick 1998). Accordingly, rhizosphere inoculation with ACC deaminase-containing bacteria decreases root ACC levels and ethylene evolution (Belimov et al. 2002; Mayak et al. 2004a). Previous results indicated that ethylene is a key regulator of the colonization of plant tissue by bacteria and that this regulation is most likely mediated by its effect on the plant signaling pathways. In this context, bacterial endophytes with high locally induced ACC deaminase activities might be excellent plant growth promoters, because they ameliorate plant stress by efficiently blocking ethylene production (Cheng et al. 2007). Furthermore, IAA-producing bacteria known to stimulate plant growth might even increase plant ethylene levels (Glick 1995). To avoid the deleterious effects of ethylene, plants might actually select for ACC deaminase-producing bacteria to become endophytic, thereby lessening plant stress caused by excessive ethylene levels. The selection of such beneficial endophytes might take place at an earlier stage (Kucera 2005). Thus, colonization by bacteria with high ACC deaminase activities might reduce the stress imposed by excessive ethylene to the plant originating from biotic and abiotic stresses (Arshad 2007). Hence, IAA and ACC deaminase production are being deployed as tools for identification and screening of endophytes (Khalid et al. 2005; Shaharoona et al. 2006; Etesami et al. 2014a, b). Therefore, trait of ACC utilization ability as a nutrient substance gives ACC deaminase-producing isolates advantages in more colonization and increase of root length of plants (Etesami et al. 2014a, b). For example, presence of PGPRs containing ACC deaminase on the roots of legume could

suppress accelerated endogenous synthesis of ethylene during the rhizobial infection and thus may facilitate nodulation. Therefore, co-inoculation of legumes with competitive rhizobia and PGPRs containing ACC deaminase could be an effective and novel approach to achieve successful and dense nodulation in legumes. It is highly expected that inoculation with PGPRs containing ACC deaminase hydrolyzed endogenous ACC instead of ethylene and subsequently legume plant as well as nodulation can be promoted (Garcia Lucas et al. 2004; Remans et al. 2007). ACC deaminase-containing PGPRs can derepress the expression of auxin response genes in the shoots (Glick et al. 2007) and also suppress the expression or functioning of other plant signaling molecules such as jasmonic acid and giberellin (Czarny et al. 2006; Cheng et al. 2010). Therefore, these bacteria may have a competitive edge over other microorganisms in the rhizosphere because of use of ACC (Glick and Bashan 1997) that helps plants to overcome many detrimental effects of biotic and abiotic stresses (Glick et al. 2007; Saleem et al. 2007). In general, a decreased level of ACC results in a lower level of endogenous ethylene, which eliminates the inhibitory effect of high ethylene concentrations (Shaharoona et al. 2006) and contribute to their root colonization (Etesami et al. 2014a).

16.3 IAA and ACC Deaminase-Producing PGPRs in Phytoremediation

Phytoremediation is the direct use of green plants and their associated microorganisms to stabilize or reduce contamination in soils, sludges, sediments, surface water, or ground water. Plant species are selected for use based on factors such as ability to extract or degrade the contaminants of concern, adaptation to local climates, high biomass, depth root structure, compatibility with soils, growth rate, ease of planting and maintenance, and ability to take up large quantities of water through the roots. Since the activity of inoculated microbes is necessary to exhibit beneficial traits for improving the plant growth and overall phytoremediation process in metal contaminated soils, the colonization and survival in metal stress field environment are considered as important factors. Plant-associated bacteria can potentially improve phytoextraction by altering the solubility, availability, and transport of heavy metal and nutrients by reducing soil pH, release of chelators, P solubilization or redox changes (Gadd 2000, 2004). In addition to improving plant's nutrient uptake and growth, the plant-associated microbes alleviate heavy metal toxicity by reducing stress ethylene production. In general, heavy metal stress induces endogenous ethylene production in plants, which can affect the root growth and consequently the growth of the whole plant. Under such conditions, in order to maintain the equilibrium between the rhizosphere and root interior ACC levels, the plants release more ACC through exudation and thus results decrease in the production of stress ethylene (Adams and Yang 1979). Recent studies have revealed that plants inoculated with PGPRs containing ACC were better able to thrive in metal

polluted soils (Rodriguez et al. 2008). Madhaiyan et al. (2007) reported that *M. oryzae* strain CBMB20 having ACC deaminase activity increased the growth of tomato seedlings grown in Ni and Cd polluted soils. The bacterium reduced the production of ethylene, which was otherwise stimulated when seedlings were challenged with increasing Ni and Cd. Zhang et al. (2011) have also confirmed that Pb-resistant and ACC deaminase-producing endophytic bacteria conferred metal tolerance onto plants by lowering the synthesis of metal-induced stress ethylene and promoted the growth of rape. Ma et al. (2011b) have also observed similar results in the case of *Allysusm serpyllifolium* and *Brassica juncea* growth under Ni stress in response to inoculation with ACC deaminase-producing endophytic bacteria. We anticipate that manipulating the rhizosphere processes for example increasing rhizosphere microbial population (by IAA-producing bacteria), inoculating the microbial strains with various PGP features as well as co-inoculating ecologically diverse microbes would yield better results for effective phytoremediation. In view of role of bacterial IAA and ACC deaminase activity in stimulation of root elongation and biomass production, increasing root exudates, enhancing plant tolerance to stresses, decreasing stresses and effective colonization, IAA and ACC deaminase-producing PGPRs can be used for effective phytoremediation of contaminated soil environment (Arshad and Frankenberger 2002; Glick et al. 2007; Saleem et al. 2007) (Fig. 4).

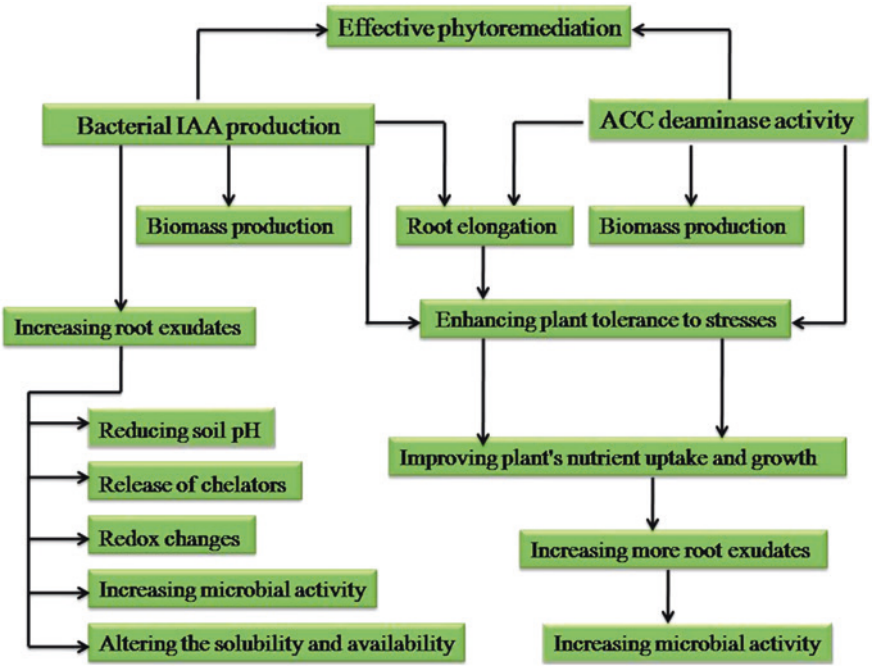

Fig. 4 Acceleration of phytoremediation by IAA and ACC deaminase-producing PGPR. Abbreviations: indole-3-acetic acid (IAA), 1-aminocyclopropane-1-carboxylate (ACC)

17 Mechanism of Action of IAA-Producing Bacteria in Nitrogen Uptake

The mechanism most often invoked to explain the direct effects of PGP bacteria on plants is the production of phytohormones, including IAA (Brown 1974; Patten and Glick 1996, 2002). The IAA containing PGPRs stimulate root proliferation and increase the root surface area or the general root architecture (Biswas et al. 2000; Lucy et al. 2004; Aloni et al. 2006). These bacteria enhance uptake of soil minerals and nutrients by the host plant. The plants growing better in turn release higher amounts of C in root exudates. The release of more C prompts increase in microbial activity, and this process continues in a cycle. The whole process makes more N available from the soil pool, influencing N flux into plant roots, and the plant is able to take up more available N (Adesemoye et al. 2009) (Fig. 5).

For various PGPRs, it has been demonstrated that enhanced root proliferation is related to bacterial IAA biosynthesis. The plant growth promotion observed after inoculation with *A. brasilense* is mainly caused by biosynthesis and secretion of bacterial IAA. In addition to providing the mechanical support and facilitating water and nutrient uptake, plant roots also synthesize, accumulate and secrete a diverse array of compounds (Walker et al. 2003). Because of

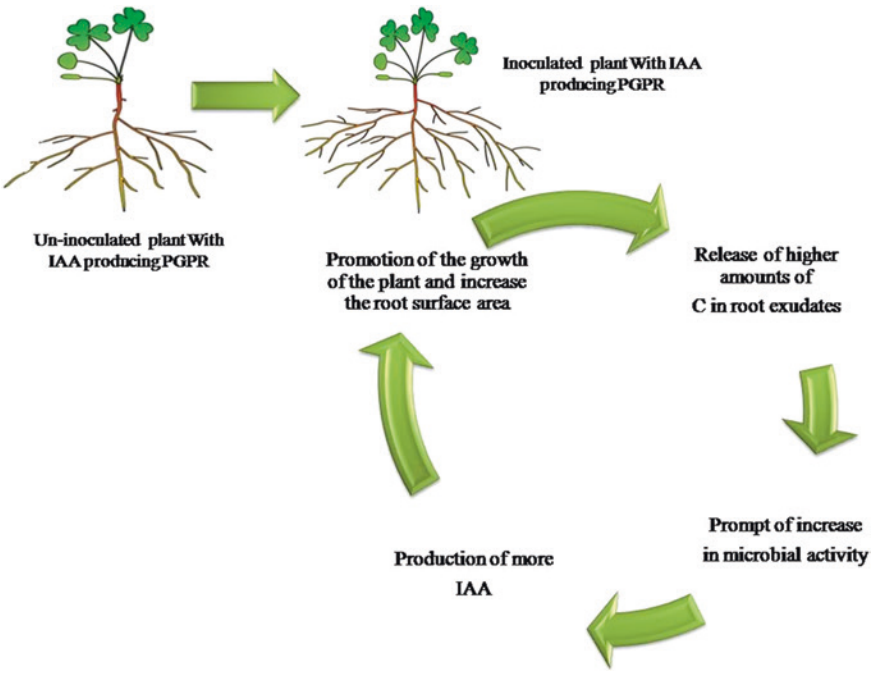

Fig. 5 Action mechanism of IAA-producing bacteria in uptake of nitrogen

the growth and development of the root system by bacterial IAA, an extremely diverse range of organic and inorganic compounds (substantial amounts of C- and N-containing compounds) can be taken up or released by seeds and roots into the soil. Microorganisms are attracted to this nutritious environment and use the root exudates and lysates for growth and multiplication on the surface of root and in the adjacent rhizosphere soil. These compounds secreted by plant roots act as chemical attractants for a vast number of heterogeneous, diverse and actively metabolizing soil microbial communities. Many organic compounds and enzymes are released by plants in root exudates that Faure et al. (2009) have reviewed their functions in the rhizosphere. Through the exudation of a wide variety of compounds, roots may regulate the soil microbial community in their immediate vicinity, cope with herbivores, encourage beneficial symbioses, change the chemical and physical properties of the soil and inhibit the growth of competing plant species (Nardi et al. 2000). Moreover, the microbial community influences the composition of the exudates to its advantage (Paterson et al. 2006; Shaw et al. 2006). The exudation of a wide range of chemical compounds modifies the chemical and physical properties of the soil and thus regulates the structure of soil microbial community in the immediate vicinity of root surface (Dakora and Phillips 2002). A fraction of these plant-derived small organic molecules is further metabolized by microorganisms in the vicinity as carbon and nitrogen sources, and some microbe-oriented molecules are subsequently retaken up by plants for growth and development (Kang et al. 2010). Indeed, carbon fluxes are critical determinants of rhizosphere function. It is reported that approximately 5–21 % of photosynthetically fixed carbon is transported to the rhizosphere through root exudation (Marschner 1995). The higher plant root system significantly contributes to the establishment of the microbial population in the rhizosphere (Dakora and Philips 2002). PGPRs often help increase root surface area to increase nutrient uptake and in turn enhance plant production (Mantelin and Touraine 2004). Application of several genera, such as *B. licheniformis* RC02, *Rhodobacter capsulatus* RC04, *Paenibacillus polymyxa* RC05, *P. putida* RC06, *Bacillus* OSU-142, *B. megaterium* RC01 and *Bacillus* M-13, showed increased root and shoot weight along with nutrient uptake in barley (Cakmacki et al. 1999). Studies with *Azospirillum* mutants altered IAA production support the view that increased rooting is caused by *Azospirillum* IAA synthesis (Dobbelaere et al. 1999). This increased rooting enhances plant mineral uptake and root exudation, which in turn stimulates bacterial colonization and thus amplifies the inoculation effect (Dobbelaere et al. 1999; Lambrecht et al. 2000; Steenhoudt and Vanderleyden 2000). It was demonstrated that *M. fujisawaense* promoted root elongation in canola (Madhaiyan et al. 2006). Ghosh et al. (2003) observed that *Bacillus circulans* DUC1, *B. wrmus* DUC2 and *Bacillus globisporus* DUC3 enhanced root and shoot elongation in *Brassica campestris*. Some compounds identified in root exudates that have been shown to play an important role in root microbe interactions include flavonoids present in the root exudates of legumes that activate *Rhizobium meliloti* genes responsible for the nodulation process (Peters et al. 1986).

17.1 IAA and ACC Deaminase in Reduced Application Rates of Chemical Fertilizers

Some chemical fertilizers have low use efficiency, meaning that only a portion of the applied nutrients are taken up by plants (Gyaneshwar et al. 2002) especially in the case of phosphorous fertilizers. One of the important mechanisms for the beneficial effects of PGPRs is stimulated nutrient availability and increase in nutrient use efficiency. Overall, results suggest that inoculants could be used to allow reductions in the current high rates of fertilizer and the resulting environmental problems (Malakoff 1998; Gyaneshwar et al. 2002; Shaharooma et al. 2008) without compromising plant productivity. In addition, under stress conditions resulting from reduced rates of inorganic fertilizers, ACC deaminase activity might have produced better root growth in the initial stages of crop growth. There has also been much recent interest in using PGPRs inoculants to decrease the application of chemical fertilizers (Adesemoye et al. 2009), either by stimulating root growth (thereby increasing root foraging for nutrients) or by directly stimulating plant nutrient uptake. Some ACC deaminase-containing PGPRs increased shoot and grain nutrient concentrations in specific plant–microbe interactions: pea and *Pseudomonas brassicacearum* Am3, *Pseudomonas marginalis* Dp1, or *Rhodococcus* sp. Fp2 (Safronova et al. 2006); peanut (*Arachis hypogea*) and various *Pseudomonas* spp. isolates (Dey et al. 2004); and wheat (*Triticum aestivum*) and *A. brasilense* Sp245 (Creus et al. 2004). Therefore, the PGPRs enhance the access of plants to the nutrient and more uptake of it by increasing the root growth of plant. For example, applied N can be lost through nitrate leaching (Biswas et al. 2000). However, a plant with a good root growth can uptake more nutrient than the same plant without a good root growth during a given period (Fig. 5). In a study, Adesemoye et al. (2009) showed PGPRs or combinations of PGPRs and Arbuscular mycorrhizal fungi (AMF) can improve the nutrient use efficiency of fertilizers. When the percentage of recommended fertilizer was reduced and inoculants were used, plant growth parameters and nutrient uptake were comparable to those with the full rate of fertilizer without inoculants. After testing different reduced fertilizer rates, under these experimental conditions, 75 % fertilizer was the stable minimum to which fertilizer could be reduced if supplemented with PGPRs to achieve growth equivalent to 100 % fertilizer without PGPRs. Shaharoona et al. (2008) reported that N use efficiency increased in response to inoculation with *P. fluorescens* at all fertilizer levels in wheat, causing 115, 52, 26 and 27 % increase over the noninoculated control at N, P and K application rates of 25, 50, 75 and 100 % recommended doses, respectively. Plants inoculated with the PGPRs together with one-third of the normal rate (33 kg N ha^{-1}) gave the highest storage root dry weight compared to noninoculated control sweet potato plants. Inoculation also increased the concentrations of N, P and K in shoots and storage root (Farzana et al. 2007). Many reports indicated that the enhancement of N uptake by plants inoculated with the PGPRs strains was not via associative N fixation (Malakoff 1998; Gyaneshwar et al. 2002; Shaharooma

et al. 2008; Adesemoye et al. 2009) and the resulting enhancement of N uptake has been attributed to alternative bacterial effects. Use of mutant strains (carrying nif D::kan interposan mutation that prevents N fixation entirely) proved the participation of *Gluconacetobacter diazotrophicus* in N fixation. It is an established fact that the growth hormones, auxins (IAA), cytokinins and gibberellins, play a role in enhancing the growth of grasses associated with diazotrophs (Bottini et al. 2004). Apart from N fixation, *G. diazotrophicus* is also reported to benefit sugarcane through production of PGP factors (Fuentes-Ramirez et al. 2001). As previously suggested, the effect of *Azotobacter* and *Azospirillum* species is attributed not only to the amounts of fixed nitrogen but also to the production of plant growth regulators such as IAA, gibberellic acid, cytokinins and vitamins (Rodelas et al. 1999; Arkhipova et al. 2007). Similarly, *Azospirillum* is also known to secrete phytohormones, induce root cell differentiation and increase water uptake (Bashan and Holguin 1997). As stated earlier, Gyaneshwar et al. (2001) also showed inoculation of *S. marcescens* IRBG500 with rice variety IR72 resulted in a significant increase in root length and root dry weight but not in total N content of rice, suggesting that the growth promotion was probably due to mechanisms other than N_2 fixation. Furthermore, *S. marcescens* IRBG500 did not show acetylene reduction activity (ARA) in association with rice.

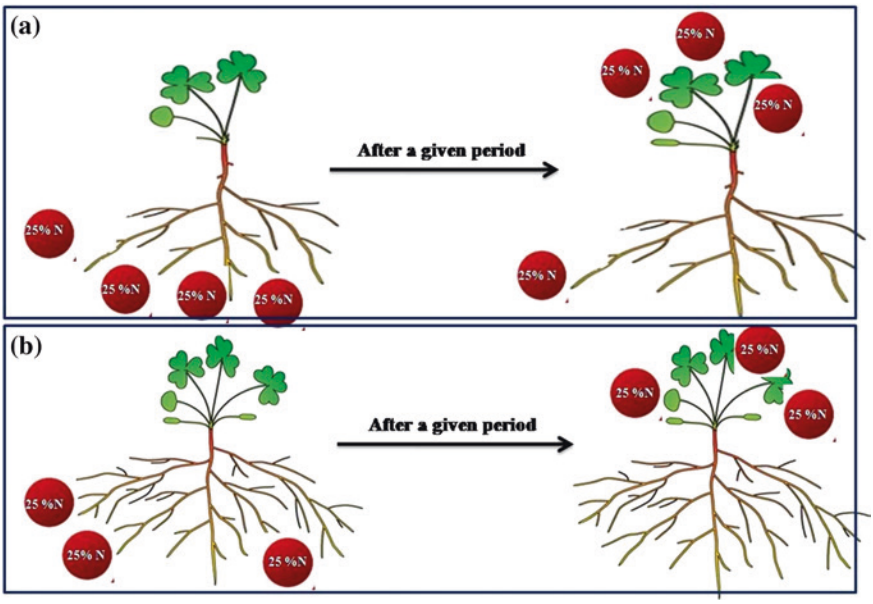

Fig. 6 Improving the nutrient use efficiency of N-fertilizers by IAA-producing PGPR. **a** 100 % recommended fertilizer without IAA-producing PGPR. **b** 75 % recommended fertilizer with IAA-producing PGPR. IAA-producing PGPR by increasing root surface area led to reduction of the percentage of recommended fertilizer (25 % reduction). Nutrient (N) uptake was comparable to those with the full rate of fertilizer without inoculants (75 % N in each plant) during a given period

Enhanced root growth following *V. paradoxus* 5C-2 inoculation probably improved nutrient uptake. These nutritional effects seem partially specific to *V. paradoxus* 5C-2, as other ACC deaminase-containing PGPRs (*P. brassicacearum* Am3, *P. marginalis* Dp1, or *Rhodococcus* sp. Fp2) had positive effects on pea foliar N, Ca, S and Fe concentrations (Safronova et al. 2006). A combination of the activities of plant and inoculants may be proposed as a model for PGPRs-enhanced N uptake in plants (Adesemoye et al. 2009) (Fig. 5). PGPRs promote the growth of the plant and increase the root surface area or the general root architecture (Biswas et al. 2000; Lucy et al. 2004). Plants growing better in turn release higher amounts of C in root exudates. The release of more C prompts increase in microbial activity and this process continues in a cycle. The whole process makes more N available from the soil pool, influencing N flux into plant roots and the plant is able to take up more available N. Figure 6 shows Improving the nutrient use efficiency of N-fertilizers by IAA-producing PGPR.

18 Co-inoculation of Multiple PGPR Strains as Way to Enhance the Performance of PGPR

Because soil is an unpredictable environment, the effect of PGPRs in crop productivity varies under laboratory, greenhouse and field trials. Climatic variations also have a large impact on the effectiveness of PGPRs but sometimes unfavorable growth conditions in the field are to be expected as normal functioning of agriculture (Zaidi et al. 2009a). To overcome the inconsistencies, one way that some previous studies have used to enhance the performance of PGPRs is co-inoculation of multiple PGPRs strains (Belimov et al. 1995; Raupach and Kloepper 2000; Bai et al. 2003; Kloepper et al. 2007; Pandey and Maheshwari 2007b; Elkoca et al. 2008). The best PGPRs may use multiple mechanisms of action on plant growth. Studies showed a promising trend in the field of inoculation technology, which is the use of mixed inoculants or application of consortia (combinations of microorganisms) that interact synergistically are currently being devised (Parmar and Dadarwal 1999; Steenhoudt and Vanderleyden 2000; Kumar et al. 2007; Rokhzadi et al. 2008; Yadegari et al. 2008; Pirlak and Kose 2009). Tittabutr et al. (2008) conducted such a study to evaluate effect of ACC deaminase activity on nodulation and growth of *Leucaena leucocephala*. Further, Remans et al. (2007) examined the potential of ACC deaminase producing PGPRs to enhance nodulation of common bean (*P. vulgaris*). Shaharoona et al. (2006) observed that co-inoculation with *Pseudomonas* and *Bradyrhizobium* species significantly improved root length, total biomass and nodulation in mung bean. Co-inoculation of a variety of PGPRs such as *Azotobacter chroococcum* and *P. putida* with *Rhizobium* sp. (AR-2-2 k) showed increased plant growth, nodulation and improved nitrogenase activity. The association of *Rhizobium* sp. with *P. putida*, *P. fluorescens* and *Bacillus cereus* seem to produce the best agronomical results (Tilak and Ranganayaki 2006). Belimov et al. (1995) reported significantly greater uptake of P in shoot

of barley with co-inoculation of *A. lipoferum* 137 and *Arthrobacter mysorens* 7 or *A. lipoferum* 137 and *Agrobacterium radiobacter* 10 than single inoculation of any of the three organisms. Microbial interaction studies performed without plants indicate that some bacterial genera allow each other to interact synergistically providing nutrients, removing inhibitory products and stimulating each other through physical or biochemical activities that may enhance some beneficial aspects of their physiology such as nitrogen fixation (Pandey and Maheshwari 2007; Arora et al. 2008). Plant studies have shown that these beneficial effects of *Azospirillum* on plants can be enhanced by co-inoculation with other microorganisms (Alagawadi and Gaur 1992; Belimov et al. 1995). Co-inoculation frequently increased growth and yield compared to single inoculation, which provided the plants with more balanced nutrition and improved absorption of nitrogen, phosphorus and mineral nutrients (Kumar et al. 2009). There is a great advantage of using phosphate-solubilizing bacteria in co-inoculation with rhizobia. This is because increased P mobilization in soil improves P deficiency. Deficit P severely limits plant growth and productivity particularly with legumes, where both plants and their symbiotic bacteria are affected. Iron availability is one of the limiting factors for poor rhizospheric colonization. The successful performance of rhizobial inoculant strain depends upon their capability to outcompete the indigenous soil bacteria, survive, propagate and enter into effective symbiosis with host plant. Many studies have indicated that efficient utilization of siderophores by rhizobia is a positive fitness factor with respect to its survival in soil (Carson et al. 2000). Further, Joshi et al. (2009) observed increase in nodule occupancy and higher rhizospheric colonization by pigeon pea-nodulating rhizobia expressing engineered siderophore cross-utilizing abilities. Thus, iron availability is one of the major factors determining rhizospheric colonization. This fact is further evidenced by work of Mahmoud and Abd-Alla (2001) where authors showed that co-inoculation of siderophore-producing PGPRs significantly enhanced nodulation and nitrogen fixation in mung bean compared to plants infected with rhizobial strain alone. There are more reports that specific siderophore-producing PGPRs stimulated the nodulation, nitrogen fixation and plant growth of leguminous plants (Grimes and Mount 1987; Omar and Abd-Alla 1994; Shenker et al. 1999). Application of PGPRs could not only produce significant benefits that require minimal or reduced levels of fertilizers but also consequently produce a synergistic effect on root growth and development (Kumar et al. 2009). Figueiredo et al. (2008) reported increased plant growth, N content and nodulation of *P. vulgaris* L. under drought stress due to co-inoculation of *Rhizobium tropici* and *P. polymyxa*. *P. vulgaris* (common bean) plants inoculated with *Rhizobium etli* overexpressing trehalose-6-phosphate synthase gene had more nodules with increased nitrogenase activity and high biomass compared with plants inoculated with wild-type *R. etli*. Three weeks old plants subjected to drought stress fully recovered, whereas plants inoculated with a wild-type *R. etli* did not survive. Decreased ethylene levels allow the plant to be more resistant to a wide variety of environmental stresses. Indeed PGP microorganisms have multifaceted beneficial effects (Avis et al. 2008) that can complement each other due to multifarious phenomenon (Maheshwari et al. 2014).

19 Biological Fertilizers Based on Bacterial Hormones

Chemical fertilizers are essential components of modern agriculture because they provide essential plant nutrients. For example, rice is the most important staple food in several developing countries and chemical fertilizers (especially N) are the most important input required for its cultivation. However, overuse of the fertilizers can cause unanticipated environmental impacts. The search for microorganisms that improve soil fertility and enhance plant nutrition has continued to attract attention due to the increasing cost of fertilizers and some of their negative environmental impacts. One potential way is the use PGPRs in order to make its cultivation sustainable and less dependent on chemical fertilizers. It is important to know how to use PGPRs that can biologically fix nitrogen, solubilize phosphorus and iron and induce some substances like IAA that could contribute to the improvement of plant growth. Nevertheless, PGPRs often fail to confer these beneficial effects when applied in the field, which is often due to insufficient rhizo- and/or endosphere colonization. The major limitation today for use of these organisms is the lack of consistent effects in PGP traits under field conditions. This is likely due to competition with the native microflora and environmental factors that either limit the population size (poor colonization) or activity of the PGPRs. Thus, the ability of a bacterial inoculant to promote plant growth can only be fully evaluated when they are tested in association with all of the components of the rhizosphere (Schroth and Weinhold 1986). Physical and chemical (abiotic soil factors) factors, such as soil texture, pH, nutrient status, high osmotic conditions, moisture, temperature, organic matter content and biological interactions in the rhizosphere are also known to impose stresses on microorganisms that may affect the establishment, survival and activity of certain organisms, whereas other organisms may remain unaffected (van Elsas and van Overbeek 1993; van Veen et al. 1997; Schroth and Weinhold 1986; Glick 1995). Bashan et al. (1995) demonstrated that concentrations of nitrogen, potassium and phosphate in soil are correlated with survival of *A. brasilense*. Despite inconsistency in field performance, PGPRs are considered as an alternative or a supplemental way of reducing chemical fertilizer in agroecosystem. In natural ecosystems, the behavior of introduced bacterial inoculants (e.g. PGPRs) and the subsequent expression of PGP represent a complex set of multiple interactions between introduced bacteria, associated crops and indigenous soil microflora. The expression of a particular trait under soil conditions is governed by the interaction of the inoculant strain with the host plant, other microorganisms in the rhizosphere, environmental factors and its own genetic makeup. In general, root elongation changes qualitatively are based on the IAA level, therefore, the amount of released IAA could have an important role in modulating the plant–microbe interaction. The property of synthesizing IAA and ACC deaminase activity is considered as effective tool for screening beneficial microorganisms suggesting that IAA-producing bacteria have profound effect on plant growth (Wahyudi et al. 2011). In view of role of bacterial IAA together with ACC deaminase activity in root elongation, enhancing root surface area,

decreasing environmental stresses and more colonization, it may be suggested the production of biological fertilizer based on bacterial hormones can be effectively used for a sustainable crop management under field conditions. Production of IAA and ACC deaminase by PGPRs, result in increased root length, root surface area and number of root tips, leading to enhanced uptake of nutrients thereby improving plant health under stress conditions (IAA by better root growth and nutrient uptake and ACC deaminase by reducing stress ethylene) (Egamberdieva and Kucharova 2009).

20 Conclusion and Future Prospects

The regulation of growth and functioning of plant root systems has attracted increased scientific attention in studies which aim to increase crop production but decrease negative environmental impacts of agriculture by decreasing water and nutrient inputs (Lynch 2007; Ghanem et al. 2011). This can be achived by using ACC deaminase and IAA-producing bacteria. These PGPRs potentially offer a low cost and flexible method to increase plant growth by regulating the growth and functioning of the root system and can stimulate plant growth directly by producing or metabolizing plant hormones or enhancing plant nutrient uptake (Arshad and Frankenberger 1991; Vessey 2003; Dodd et al. 2010; Dodd and Ruiz-Lozano 2012). It has been documented that the IAA-producing bacteria together with ACC deaminase activity exert stimulatory effects on the growth of plants. The beneficial effects of these PGPRs are mostly related to the changes in IAA concentration. At the same time, modification of phytohormone levels by microbes can lead to characteristic changes in plant growth development such as phytohormones produced by the bacteria, which can increase root area, leading to higher water and other nutrients uptake from soil. These bacteria, therefore, can be effectively used for plant growth improvement.

Further investigations about the mechanisms involved would help to improve the understanding of plant growth promotion by microorganisms. IAA accumulation in the rhizosphere contributes to an increase in the root surface area and to alterations in root exudation. As a result, plant nutrition and growth are improved, new niches for plant colonization by the bacteria are formed, and bacterial IAA production is corrected again. A better understanding of the basic principles of the rhizosphere ecology, including the function and diversity of inhabiting microorganisms is on the way but further knowledge is necessary to optimize soil microbial technology to the benefit of plant growth and health in the natural environment. Therefore, current production methods in agriculture, e.g. the improper use of chemical pesticides and fertilizers creating a long list of environmental and health problems, should be reduced. Our understanding of plant–microbe interactions in rhizosphere must increase before we can presume that utilization of PGPRs as biofertilizers will determine a sustainable promotion of host plants growth. While considerable research has demonstrated their potential utility, the

successful application of PGPRs in the field has been limited by a lack of knowledge of ecological factors that determine their survival and activity in the plant rhizosphere. Therefore, the practical application of these techniques should be further evaluated in field experiments.

The finding that IAA is used as a signal for gene regulation in some bacteria, both in IAA producers and nonproducers further supports the idea of IAA being part of genetic networks in some microorganisms. When these microorganisms interact with plants as part of their ecological habitat, it becomes obvious that a reciprocal IAA-mediated signaling process in microbe–plant interactions is likely to occur (Lambrecht et al. 2000). Our further understanding of bacteria–plant interactions be it pathogenic or beneficial, needs detailed studies that examine hormonal dynamics throughout the course of the interaction. Nevertheless, these conditions were removed from real conditions where the inoculum strain has to compete with a wide variety of soil microorganisms. Therefore, experiments under real conditions are necessary to clarify if the strain is able to promote the growth of plants under real soil conditions. However, the application of inocula in agriculture needs further research to better understand the interactions between plants and microorganisms. Not only is it necessary to provide the right microorganisms, but also the correct techniques to check the fate of the inoculum in order to establish the most suitable way to use the microorganisms in agriculture. The lack of such information has been shown to be the main cause of failure in the use of PGPRs. It is also suggested that PGPRs need to be reinoculated every year/season as they will not live forever in the soil. A large body of knowledge suggests that root exudates may act as messengers that communicate and initiate biological and physical interactions between roots and soil organisms. Although root exudation clearly represents a significant carbon cost to the plant, the mechanisms and regulatory processes controlling root secretion are just now beginning to be examined. In conclusion, this review and our studies (Etesami et al. 2014a, b, 2015) also signify that screening of effective bacterial strains under controlled conditions based on IAA and ACC deaminase production and growth promotion may be a useful strategy for the selection of efficient isolates.

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