

# Chapter 2

## Mechanisms Used by Plant Growth-Promoting Bacteria

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### 2.1 Introduction

The world population, currently ~7 billion, continues to increase so that by 2020 it is estimated to reach ~8 billion. There is a real concern regarding our ability to feed all of these people, an endeavor that requires that agricultural productivity continues to increase. Thus, more than ever, obtaining high yields is the main challenge for agriculture. In addition, in recent years both producers and consumers have increasingly focused on the health and quality of foods, as well as on their organoleptic and nutritional properties.

Stimulated by increasing demand, and by the awareness of the environmental and human health damage induced by overuse of pesticides and fertilizers (Avis et al. 2008; Leach and Mumford 2008), worldwide agricultural practice is moving to a more sustainable and environmental friendly approach. As an example, the amount of organically cultivated land in the European Union increased by ~21% per year between 1998 and 2002 and has continued to expand since then. In Italy, the EU Member State with the largest number of agricultural producers and the highest number of hectares devoted to organic agriculture, consumption of organic foods increased by 11% in 2007 alone ([http://www.ec.europa.eu/agriculture/organic/eu-policy/data-statistics\\_it](http://www.ec.europa.eu/agriculture/organic/eu-policy/data-statistics_it)).

In this context, soil microorganisms with beneficial activity on plant growth and health represent an attractive alternative to conventional agricultural (Antoun and Prévost 2005). In recent years, several microbial inoculants have been formulated,

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produced, marketed, and applied successfully by an increasing number of growers (Reed and Glick 2004).

Although all parts of the plant are colonized by microorganisms, the rhizosphere represents the main source of bacteria with plant-beneficial activities. These bacteria are generally defined as plant growth-promoting bacteria (PGPB) (Bashan and Holguin 1998). They typically promote plant growth in two ways: direct stimulation and biocontrol (i.e., suppressive activity against soil-borne diseases) (Glick 1995). Stimulation and protection of different crops by PGPB has been demonstrated many times under controlled conditions and field trials and a large number of papers on this topic are available (reviewed by Reed and Glick 2004). The positive effect of many soil bacteria on plants is mediated by a range of mechanisms including improvement of mineral nutrition, enhancement of plant tolerance to biotic and abiotic stress, modification of root development, as well as suppression of soil-borne diseases (Glick 1995; Glick et al. 1999; Kloepper et al. 1989). The bacterial traits involved in these activities, include nitrogen fixation, phosphate solubilization, iron sequestration, synthesis of phytohormones, modulation of plant ethylene levels, and control of phytopathogenic microorganisms.

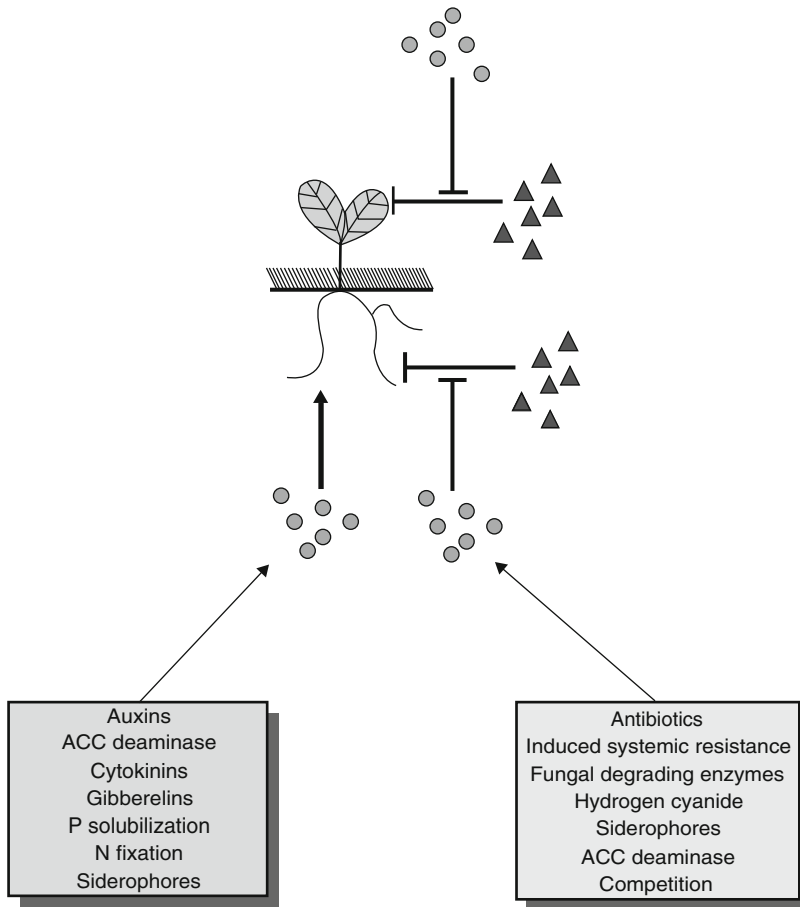
This chapter provides an overview of the main mechanisms used by PGPB (Fig. 2.1). In the first section, the mechanisms involved in plant-growth promotion via mineral nutrition improvement are described with special reference to nitrogen fixation, phosphate solubilization, and iron chelation. In the second section, the effects of phytohormones whose levels are modulated by PGPB, auxins, cytokinins, and gibberellins, which are synthesized by PGPB, and the enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase, which lowers plant ethylene levels, on plant growth and development are discussed. The ability of some PGPB to inhibit the growth of phytopathogens via competition for nutrients or colonization sites, the synthesis of antibiotics and lytic enzymes, and induced systemic resistance is discussed in the third section. Finally, given the very large body of literature in this area, for the most part, our attention is focused on the more recent literature.

## 2.2 Provision of Nutrients

Plant growth promotion by bacteria can also occur as a consequence of the provision of nutrients that are not sufficiently available in the soil; these nutrients include phosphate, nitrogen, and iron. The main mechanisms involved, as explained below, are the solubilization of phosphate, nitrogen fixation, and iron chelation through siderophores.

### 2.2.1 Phosphate Solubilization

Although the amount of phosphorus (P) usually in soil is between 400 and 1,200 mg kg<sup>-1</sup> of soil, the concentration of soluble P in soil is typically ~1 mg kg<sup>-1</sup>



**Fig. 2.1** Facilitation of plant growth by plant growth-promoting bacteria (PGPB). The PGPB (circles) may either promote plant growth directly (arrow), generally by first interacting with plant roots, or indirectly ( $\perp$ ) by preventing pathogens (triangles) from damaging the plant. Some of the bacterial traits/mechanisms that contribute to direct and indirect plant growth promotion are highlighted. Similar PGPB traits contribute to the biocontrol of root and leaf pathogens

or less (Goldstein 1994). P in soil is present in two main insoluble forms: mineral forms such as apatite, hydroxyapatite, and oxyapatite, and organic forms including inositol phosphate (soil phytate), phosphomonoesters, phosphodiester, and phosphotriesters (Khan et al. 2007).

Since P is an essential macronutrient for plant growth and has only limited bioavailability, it is considered to be one of the elements that limits plant growth (Feng et al. 2004). To satisfy plants' nutritional requirements, P is usually added to soils as fertilizers synthesized through high-energy-intensive processes (Goldstein et al. 1993). However, plants can use only a small amount of this P since 75–90% of added P is precipitated by metal–cation complexes, and rapidly becomes fixed in

soil. Thus, solubilization and mineralization of P by phosphate-solubilizing bacteria (PSB) is one of the most important bacterial physiological traits in soil biogeochemical cycles (Jeffries et al. 2003), as well as in plant growth promotion by PGPB (Rodriguez and Fraga 1999; Richardson 2001).

The major mechanism used by PSB for solubilization of inorganic P is based on the synthesis of low molecular weight organic acids such as gluconic and citric acid (Bnayahu 1991; Rodriguez et al. 2004). These organic acids bind phosphate with their hydroxyl and carboxyl groups thereby chelating cations and also inducing soil acidification, both resulting in the release of soluble phosphate (Kpombrekou and Tabatabai 1994; Bnayahu 1991). Other mechanisms that have been implicated in solubilization of inorganic phosphate are the release of  $H^+$  (Illmer and Schinner 1992), the production of chelating substances (Sperber 1958; Duff and Webley 1959) and inorganic acids (Hopkins and Whiting 1916). In addition, exopolysaccharides synthesized by PSB participate indirectly in the solubilization of tricalcium phosphates by binding free P in the medium, affecting the homeostasis of P solubilization (Yi et al. 2008).

The mineralization of organic P occurs through the synthesis of phosphatases, including phosphomonoesterase, phosphodiesterase, and phosphotriesterase, catalyzing the hydrolysis of phosphoric esters (Rodriguez and Fraga 1999). In addition, P solubilization and mineralization can coexist in the same bacterial strain (Tao et al. 2008).

Genera able to solubilize phosphate include *Pseudomonas* (Di Simine et al. 1998; Gulati et al. 2008; Park et al. 2009; Malboobi et al. 2009), *Bacillus* (De Freitas et al. 1997; Toro et al. 1997; Rojas et al. 2001; Sahin et al. 2004), *Rhizobium* (Halder et al. 1991; Abd-Alla 1994; Chabot et al. 1996), *Burkholderia* (Tao et al. 2008; Jiang et al. 2008), *Enterobacter* (Toro et al. 1997; Sharma et al. 2005), and *Streptomyces* (Molla et al. 1984; Mba 1994; Hamdali et al. 2008; Chang and Yang 2009). Recently, the potential of nonstreptomycete actinomycetes to solubilize insoluble phosphates in soil and to promote plant growth has been investigated (El-Tarabily et al. 2008). In particular, a highly rhizosphere competent isolate of *Micromonospora endolithica* able to solubilize considerable amounts of P, to produce acid and alkaline phosphatases as well as several organic acids, was found to be unable to synthesize any other stimulatory compounds (such as auxin, cytokinin, and gibberellin) and yet promoted the growth of beans.

The role of phosphate solubilization in plant growth promotion is often overshadowed by other plant beneficial activities expressed by the PSB. When Poonguzhali et al. (2008) selected ten pseudomonads on the basis of their high phosphate solubilization activity on tricalcium phosphate and inoculated seeds with these strains, which also synthesize indole-3-acetic acid, ACC deaminase, and siderophores, the plants showed increased root elongation and biomass, however, under the conditions employed, P uptake was unaffected. Notwithstanding the difficulty that sometimes exists in pinpointing the contribution of phosphate solubilization activity to plant growth promotion, numerous reports demonstrate direct connections between phosphate solubilization activity and increased P in tissues of plants inoculated with PSB (Rodriguez and Fraga 1999).

Besides the low rhizospheric competence of some PSB strains, specificity for the host plant or soil type could play a role. For example, solubilization of Ca–P complexes is quite prevalent among PSB, whereas the release of P by Fe–P or Al–P is very rare. Thus, release of soluble P is prevalent in calcareous soils and low in alfisols (Gyaneshwar et al. 2002). Frequently, the relatively high PSB density in soil does not correspond to the amount of soluble P present in soil. The efficiency of various PSB also depends upon their physiological status, and the level of P released by phosphate solubilization is considered to be inadequate to induce a substantial increase of biomass. To obviate this problem, plants are often inoculated with PSB at concentrations that are higher than what is normally present in soil.

As a consequence of the heterogeneous results obtained by inoculating plants with PSB, the commercial application of PSB-based biofertilizers has been quite limited. Longer bacterial survival of PSB may be achieved by cell encapsulation inside nontoxic polymers such as alginate that increase the shelf life of the bacteria, protect them against many environmental stresses, and release them to the soil gradually (Bashan and Gonzalez 1999; Bashan et al. 2002). This may be more effective than the application of cell suspensions (Vassileva et al. 2000, 2006a, b; Vassilev and Vassileva 2004) with, e.g., improvement of growth promotion efficacy related to enhanced phosphate solubilization activity in lettuce (*Lactuca sativa*) inoculated with encapsulated but not free-living *Enterobacter* sp. cells (Vassileva et al. 1999).

The highest efficiency in stimulating plant growth was observed when PSB were co-inoculated with bacteria with other physiological capabilities such as N fixation (Rojas et al. 2001; Valverde et al. 2006; Matias et al. 2009), or with mycorrhizal (Ray et al. 1981; Azcón-Aguilar et al. 1986; Toro et al. 1997; Babana and Antoun 2006; Matias et al. 2009) or nonmycorrhizal fungi (Babana and Antoun 2006). Thus, the use of mixed inocula with different plant beneficial activities appears to be a promising strategy. In one set of experiments, increased amounts of both nitrogen fixation and phosphate solubilization were observed in mangrove seedlings treated with a mixture of the nitrogen-fixing *Phyllobacterium* sp. and the PSB *Bacillus licheniformis*, compared to plants inoculated with individual cultures (Rojas et al. 2001). In fact, when the two bacterial species were cocultivated in vitro, they affected one another's metabolism: N fixation increased in *Phyllobacterium* sp., and phosphate solubilization increased in *B. licheniformis*. However, the growth of the coinoculated plants did not differ from that of plants treated with a single bacterium.

Finally, the genetic manipulation of PGPB to obtain expression or over-expression of genes involved in phosphate solubilization is an attractive strategy for improving the efficacy of some bacterial inoculants. With this approach, it may be possible to avoid competition among microorganisms that is often observed when mixed inoculants are employed. Unfortunately, largely for political rather than scientific reasons, the deliberate release of genetically modified organisms to the environment is still controversial in many jurisdictions (Rodriguez et al. 2006).

### 2.2.2 Iron Chelation and Siderophores

Iron is the fourth most abundant element on earth (Ma 2005); however, in aerobic soils, iron is mostly precipitated as hydroxides, oxyhydroxides, and oxides so that the amount of iron available for assimilation by living organisms is very low, ranging from  $10^{-7}$  to  $10^{-23}$  M at pH 3.5 and 8.5, respectively. Both microbes and plants have a quite high iron requirement (i.e.,  $10^{-5}$  to  $10^{-7}$  and  $10^{-4}$  to  $10^{-9}$  M, respectively), and this condition is more accentuated in the rhizosphere where plant, bacteria, and fungi compete for iron (Guerinot and Ying 1994; Loper and Buyer 1991). To survive with a limited supply of iron, in bacteria, cellular iron deficiency induces the synthesis of low-molecular weight siderophores, molecules with an extraordinarily high affinity for  $\text{Fe}^{+3}$  ( $K_a$  ranging from  $10^{23}$  to  $10^{52}$ ) as well as membrane receptors able to bind the Fe–siderophore complex, thereby allowing iron uptake by microorganisms (Neilands 1981).

Many *Pseudomonas* spp. and related genera produce yellow–green, water soluble, fluorescent pigments collectively called pyoverdines, composed of a quinoleinic chromophore bound together with a peptide and an acyl chain, conferring a characteristic fluorescence to the bacterial colonies (Meyer and Abdallah 1978). About 100 different pyoverdines have been identified (Budzikiewicz 2004; Meyer et al. 2008) and represent about 20% of the microbial siderophores that have been characterized (Boukhalfa and Crumbliss 2002). Pyoverdine-mediated iron uptake confers a competitive advantage on to fluorescent pseudomonads over other microorganisms (Mirleau et al. 2000, 2001). Regulation of pyoverdine synthesis is not only based on iron availability but also on quorum sensing whereby cell-to-cell communication mediated by N-acyl homoserines lactones occurs activating siderophore synthesis (Stintzi et al. 1998).

In plants, active iron uptake occurs mainly through two strategies (Curie and Briat 2003). Strategy I, exploited by dicotyledonous and nongraminaceous monocotyledonous plants, is based on acidification of the rhizosphere by  $\text{H}^+$  excretion, leading to the reduction of  $\text{Fe}^{+3}$  to  $\text{Fe}^{+2}$  and its transport inside root cells (Robinson et al. 1999; Marschner 1995; Eide et al. 1996; Vert et al. 2002). Strategy II, used in grasses and graminaceous plants including wheat (*Triticum aestivum*), barley (*Hordeum vulgare*), rice (*Oryza sativa*), and maize (*Z. mays*), relies on the synthesis of  $\text{Fe}^{+3}$  chelators called phytosiderophores and on the uptake of the Fe–phytosiderophore complex in root cells mediated by specific transporter molecules (Curie et al. 2001; Von Wirén et al. 1994). The iron dynamics in the rhizosphere are under the control of the combined effects of soil properties and plant and microbially produced compounds (Robin et al. 2008; Lemanceau et al. 2009).

Plant iron nutrition can affect the structure of bacterial communities in the rhizosphere. For example, transgenic tobacco that overexpresses ferritin and accumulates more iron than nontransformed tobacco has less bioavailable iron in the rhizosphere (Robin et al. 2006). As a consequence, the composition of the rhizosphere bacterial community differed significantly when compared to nontransformed tobacco lines.

Siderophores are involved both in plant growth promotion and health protection (Robin et al. 2008). The benefits of microbial siderophores have been demonstrated by supplying radiolabeled ferric-siderophores to plants as a sole source of iron (Crowley et al. 1988; Duijff et al. 1994a, b; Walter et al. 1994; Yehuda et al. 1996; Siebner-Freibach et al. 2003; Jin et al. 2006). The role of siderophores in plant nutrition is further supported by the absence of iron-deficiency symptoms (i.e., chlorosis) and by the fairly high iron content in roots of plants grown in nonsterile soils compared to plants grown in sterile systems (Masalha et al. 2000). Thus, mung bean (*Vigna radiata* L. Wilzeck) plants, inoculated with the siderophore-producing *Pseudomonas* strain GRP3 and grown under iron-limiting conditions, showed reduced chlorotic symptoms and an enhanced chlorophyll level compared to uninoculated plants (Sharma et al. 2003). In addition, the Fe-pyoverdine complex synthesized by *Pseudomonas fluorescens* C7 was efficiently taken up by the plant *Arabidopsis thaliana*, leading to an increase of iron content inside plant tissues and to improved plant growth (Vansuyt et al. 2007).

Plant iron nutrition improvement by soil bacteria is even more important when the plant is exposed to an environmental stress such as heavy metal pollution. Metal mobility in soil can be affected by microbial metabolites and especially by siderophores that can bind to magnesium, manganese, chromium (III), gallium (III), cadmium, copper, nickel, arsenic, lead, and zinc and radionuclides, such as plutonium (IV) as well as to iron (Malik 2004; Nair et al. 2007). In addition, by supplying iron to the plants, siderophores may help to alleviate the stresses imposed on plants by high soil levels of heavy metals (Diels et al. 2002; Belimov et al. 2005; Braud et al. 2006). *Gluyvera ascorbata*, a PGPB able to synthesize siderophores was able to protect canola, Indian mustard, canola, and tomato from heavy metal (nickel, lead, and zinc) toxicity (Burd et al. 1998, 2000). The siderophore overproducing mutant SUD165/26 of this bacterium provided even greater protection, as indicated by the enhanced biomass and chlorophyll content in plants cultivated in nickel-contaminated soil (Burd et al. 2000).

When two mutants of strain *Pseudomonas putida* ARB86, one impaired in siderophore synthesis and the other overproducing siderophores were used to inoculate *A. thaliana* plants exposed to nickel, symptoms induced by the metal were relieved to the same extent in plants inoculated with both mutants and wild type suggesting that alleviation of Ni toxicity in this case is siderophore independent (Someya et al. 2007). Similarly, two siderophore-producing bacterial strains reduced Zn uptake by willow (*Salix caprea*) suggesting that bacterial siderophores may bind to heavy metals from soil and inhibit their uptake by plants. On the other hand, enhancement of Zn and Cd uptake in willow inoculated with a *Streptomyces* strain unable to produce siderophores, highlights the importance of other physiological traits for heavy metal accumulation by *S. caprea* (Kuffner et al. 2008). The bottom line for these seemingly contradictory results is that the effect of siderophores in the presence of high concentrations of metals is quite complex, depending on soil composition, metal type and concentration, and the siderophore(s) and plant(s) utilized. Thus, the impact of siderophore in metal-contaminated soils needs to be assessed on a case by case basis.

### 2.2.3 Nitrogen Fixation

Agriculture has become increasingly dependent on chemical sources of nitrogen derived at the expense of petroleum. Besides being costly, the production of chemical nitrogen fertilizers depletes nonrenewable resources and poses human and environmental hazards. To complement and eventually substitute mineral fertilizers with biological nitrogen fixation would represent an economically beneficial and ecologically sound alternative. However, despite nitrogen's abundance in the atmosphere, it must first be reduced to ammonia before it can be metabolized by plants to become an integral component of proteins, nucleic acids, and other biomolecules (Bøckman 1997). The most important microorganisms that are currently used agriculturally to improve the nitrogen content of plants, include a range of *Rhizobia*, each specific for a limited number of plants. Other nitrogen-fixing bacteria, notably *Azospirillum* spp., are also employed as bacterial inoculants; however, it is generally thought that for free-living bacteria, the provision of fixed nitrogen is only a very small part of what the bacterium does for the plant (James and Olivares 1997).

Nitrogen-fixing (diazotrophic) bacteria fix atmospheric nitrogen by means of the enzyme nitrogenase, a two component metalloenzyme composed of (a) dinitrogenase reductase, a dimer of two identical subunits that contains the sites for MgATP binding and hydrolysis, and supplies the reducing power to the dinitrogenase, and (b) the dinitrogenase component that contains a metal cofactor (Dean and Jacobson 1992). Overall, nitrogenase biosynthesis (*nif*) genes include structural genes, genes involved in the activation of the Fe protein, iron molybdenum cofactor biosynthesis, electron donation, several genes of unknown function, and the regulatory genes required for the synthesis and function of the nitrogenase. The *nif* genes may be carried on plasmids as in most *Rhizobium* species or, more commonly, in the chromosome of free-living (Fischer 1994) and associative nitrogen-fixing bacteria (Colnaghi et al. 1997). The *nif* genes from many different diazotrophs are arranged in a single cluster of approximately 20–24 kb with seven separate operons that together encode 20 distinct proteins. All of the *nif* genes are transcribed and translated in a concerted fashion, under the control of the *nifA* and *nifL* genes. NifA protein is a positive regulatory factor which turns on the transcription of all of the *nif* operons (except its own). The DNA-bound NifA protein interacts with transcription initiation factor sigma 54 before transcription from the *nif* promoter is initiated. NifL protein is a negative regulatory factor which, in the presence of either oxygen or high levels of fixed nitrogen, acts as an antagonist of the NifA protein. Because of the complexity of the *nif* system, genetic strategies to improve nitrogen fixation have been elusive.

Since nitrogen fixation requires a large amount of ATP, it would be advantageous if rhizobial carbon resources were directed toward oxidative phosphorylation, which results in the synthesis of ATP, rather than glycogen synthesis, which results in the storage of energy as glycogen. A strain of *R. tropici* with a deletion in the gene for glycogen synthase was constructed (Marroquí et al. 2001). Treatment of bean plants with this mutant strain resulted in a significant increase in both the



number of nodules that formed and the plant dry weight in comparison with treatment with the wild-type rhizobial strain.

Oxygen is both inhibitory to nitrogenase and is a negative regulator of *nif* gene expression; however, it is required for *Rhizobia* spp. bacteroid respiration. This difficulty can be resolved by the introduction of leghemoglobin, which binds free oxygen tightly resulting in an increase in nitrogenase activity. Since the globin portion of leghemoglobin is produced by the plant, more efficient strains of *Rhizobium* spp. may be engineered by transforming strains with genes encoding bacterial hemoglobin (Ramírez et al. 1999). Following transformation of *Rhizobium etli* with a plasmid carrying the *Vitreoscilla* sp. (a gram negative bacterium) hemoglobin gene, at low levels of dissolved oxygen in the medium, the rhizobial cells had a two- to threefold higher respiratory rate than the nontransformed strain. In greenhouse experiments, when bean plants were inoculated with either nontransformed or hemoglobin-containing *R. etli* the plants inoculated with the hemoglobin-containing strain had approximately 68% more nitrogenase activity. This difference in nitrogenase activity leads to a 25–30% increase in leaf nitrogen content and a 16% increase in the nitrogen content of the seeds that are produced (Ramírez et al. 1999).

The most common strain of *R. etli* encodes three copies of the nitrogenase reductase (*nifH*) gene, each under the control of a separate promoter. To increase the amount of nitrogenase, the strongest of the three *nifH* promoters (i.e., *PnifHc*) was coupled to the *nifHcDK* operon, which encodes the nitrogenase structural genes (*nifHc* is one of the three *nifH* genes). When the *PnifHc–nifHcDK* construct was introduced into the wild-type strain, the net result was a significant increase in nitrogenase activity, plant dry weight, seed yield, and the nitrogen content of the seeds. This genetic manipulation worked as well or better when the *PnifHc–nifHcDK* construct was introduced into the Sym plasmid from *R. etli* that contains all of the *nif* genes (Peralta et al. 2004). In addition, expression of the *PnifHc–nifHcDK* construct in a poly- $\beta$ -hydroxybutyrate negative strain of *R. etli* enhanced plant growth to an even greater extent than when this construct was expressed in a wild-type poly- $\beta$ -hydroxybutyrate positive strain. This is probably because in the poly- $\beta$ -hydroxybutyrate negative strain there is an increased flux of carbon through the citric acid cycle and hence an increase in the amount of ATP to power nitrogen fixation (Peralta et al. 2004).

An undesirable side reaction of nitrogen fixation is the reduction of  $H^+$  to  $H_2$  by nitrogenase. ATP is wasted on the production of hydrogen and only 40–60% of the electron flux through the nitrogenase system is transferred to  $N_2$ , lowering the overall efficiency of nitrogen fixation. Some diazotrophic strains contain hydrogenase that can take up  $H_2$  from the atmosphere and convert it into  $H^+$  and the presence of a hydrogen uptake system in a symbiotic diazotroph improves its ability to stimulate plant growth by binding and then recycling the hydrogen gas that is formed inside the nodule by the action of nitrogenase. Although it is clearly beneficial to the plant to obtain its nitrogen from a symbiotic diazotroph that has a hydrogen uptake system, this trait is not common in naturally occurring rhizobial strains.

In *Rhizobium leguminosarum*, 18 genes are associated with hydrogenase activity. There are 11 *hup* (hydrogen uptake) genes responsible for the structural components of the hydrogenase, the processing of the enzyme, and electron transport. There are also seven *hyp* (hydrogenase pleiotropic) genes that are involved in processing the nickel that is part of the active center of the enzyme. The *hup* promoter is dependent on the NifA protein so that *hup* genes are only expressed within bacteroids. On the other hand, the *hyp* genes are transcriptionally regulated by an FnrN-dependent promoter that is turned on by low levels of oxygen so that the *hyp* genes are expressed both in bacteroids and microaerobically. By modifying the chromosomal DNA of *R. leguminosarum* and exchanging the *hup* promoter for an FnrN-dependent promoter, a derivative of the wild type with an increased level of hydrogenase was created (Ureta et al. 2005). The engineered strain displayed a twofold increase in hydrogenase activity compared to the wild type and no discernible amount of hydrogen gas was produced as a byproduct of nitrogen fixation with the net result that the amount of fixed nitrogen and hence plant productivity was greater.

A small localized rise in plant ethylene that can inhibit subsequent rhizobial infection and nodulation is often produced following the initial stages of *Rhizobia* infection. Some *Rhizobia* strains increase the number of nodules that form on the roots of a host legume by limiting the rise in ethylene either by synthesizing a small molecule called rhizobitoxine (Yuhashi et al. 2000) that chemically inhibits ACC synthase, one of the ethylene biosynthetic enzymes, or by producing ACC deaminase and removing some of the ACC before it can be converted to ethylene (Ma et al. 2002). The result of lowering the level of ethylene is that both the number of nodules and the biomass of the plant is increased by 25–40% (Ma et al. 2003). In the field, approximately 1–10% of rhizobial strains possess ACC deaminase (Duan et al. 2009) thus it is possible to increase the nodulation efficiency of *Rhizobia* strains that lack ACC deaminase by engineering these strains with isolated *Rhizobia* ACC deaminase genes (and regulatory regions). In fact, insertion of an ACC deaminase gene from *R. leguminosarum* bv. *viciae* into the chromosomal DNA of a strain of *Sinorhizobium meliloti* that lacked this enzyme dramatically increased both nodule number and biomass of host alfalfa plants (Ma et al. 2004). Because of political/regulatory considerations, genetically engineered strains of *Rhizobia* may not currently be acceptable for use in the field; however, several commercial inoculant producers are already screening their more recently isolated *Rhizobia* strains for active ACC deaminase.

## 2.3 Modulation of Phytohormone Levels

The phytohormones auxins, cytokinins, gibberellins, and ethylene and abscisic acid (ABA) all play key roles in the regulation of plant growth and development (Salisbury and Ross 1992). When plants encounter suboptimal environmental conditions, the levels of endogenous phytohormones are often insufficient for

optimal growth (De Salamone et al. 2005). In this context, some phytohormones or hormone-like substances that stimulate seed and tuber germination, root formation or fruit ripening, are included as a part of commercial plant growth stimulators (Tsakelova et al. 2006).

Many rhizosphere microorganisms produce or modulate phytohormones under in vitro conditions (De Salamone et al. 2005). Consequently, many PGPB with the ability to alter phytohormone levels can affect the plant's hormonal balance. The production of IAA, cytokinins, and gibberellins by PGPB and their effect on plant growth are discussed in Sects. 2.3.1 and 2.3.2. The modulation of ethylene synthesis by ACC deaminase-producing bacteria and their role in supporting plant growth in natural and stressed environment is described in Sect. 2.3.3.

### 2.3.1 IAA

Besides influencing division, extension, and differentiation of plant cells and tissues, auxins stimulate seed and tuber germination; increase the rate of xylem and root development; control processes of vegetative growth; initiate lateral and adventitious roots; mediate responses to light and gravity, florescence, and fructification of plants; and also affect photosynthesis, pigment formation, biosynthesis of various metabolites, and resistance to stressful conditions (Tsakelova et al. 2006). Although several naturally occurring auxins have been described, indole-3-acetic acid (IAA) is the most studied auxin, and frequently auxin and IAA are considered as interchangeable terms. However, in plants most IAA is generally present as conjugated forms that are mainly implicated in transport, storage, and protection of IAA catabolism (Seidel et al. 2006).

Different auxin 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 the developmental stage of the plant. The actual range of effective auxin concentrations varies according to plant species and to the sensitivity of the plant tissue to auxin; 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 *A. thaliana* seedlings. Moreover, the endogenous pool of auxin 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 auxin available to the plant and to the sensitivity of the host plant to the phytohormone. In addition, the level of auxin 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 auxin level to either optimal or supraoptimal, resulting in plant growth promotion or inhibition, respectively.

Production of auxin is widespread among soil bacteria (estimated to be ~80% of all soil bacteria). This ability has been detected in a wide range of soil bacteria as well as in streptomycetes, methylobacteria, cyanobacteria, and archaea. Several of these microorganisms, are involved in plant pathogenesis, whereas others are free-living or symbiotic PGPB.

Five of the six pathways for auxin biosynthesis in bacteria rely on tryptophan as the main IAA precursor. These pathways, constitutively expressed or inducible, encoded by genomic or plasmid DNA, have been classified according to their intermediate as indole-3-acetamide, indole-3-pyruvate, tryptamine, tryptophan side-chain oxidase, indole-3-acetonitrile, and tryptophan independent and they have been extensively reviewed (Patten and Glick 1996; Spaepen et al. 2007).

Auxin 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). IAA synthesized by bacteria is involved at different levels in plant–microorganism interactions: in particular, plant growth promotion and root nodulation can be affected by IAA.

One of the main effects of bacterial IAA is the enhancement of lateral and adventitious rooting leading to improved mineral and nutrient uptake and root exudation that in turn stimulates bacterial proliferation on the roots (Dobbelaere et al. 1999; Lambrecht et al. 2000; Steenhoudt and Vanderleyden 2000). The role of IAA synthesized by the PGPB *P. putida* GR12-2, which produces relatively low levels of the phytohormone, in the development of the canola roots has been studied following the construction of an IAA-deficient mutant of this strain (Patten and Glick 2002). Seed inoculation with wild-type GR12-2 induced the formation of tap roots that were 35–50% longer than the roots from seeds treated with the IAA-deficient mutant and the roots from uninoculated seeds. Conversely, inoculation of mung bean cuttings with the mutant *auxI* of the same strain, which overproduces IAA, yielded a greater number of shorter roots compared with controls (Mayak et al. 1999). This result was explained by the combined effect of auxin on growth promotion and inhibition of root elongation by ethylene (Jackson 1991). The bacterial IAA incorporated by 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 alone does not account for growth promotion capacity of *P. putida* GR12-2 (Xie et al. 1996).

Most *Rhizobium* species produce IAA (Badenochjones et al. 1983) and several studies have suggested that changes in auxin levels in the host plant are necessary for nodule organogenesis (Mathesius et al. 1998). 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 (Plazinski and Rolfe 1985; van Noorden et al. 2006). In addition, the amount of IAA in root nodules was higher than in nonnodulated roots (Badenochjones et al. 1983;

Basu and Ghosh 1998; Theunis 2005). On the other hand, mutants of *Bradyrhizobium elkanii* that were defective in IAA synthesis induced fewer nodules on soybean roots than did the wild-type strain (Fukuhara et al. 1994). Furthermore, in nodules induced by low IAA-producing mutants of *Rhizobium* sp. NGR234, the IAA content is lower than in nodules induced by the wild-type strain, supporting the idea that part of the IAA found in nodules is of prokaryotic origin (Theunis 2005).

It has been suggested that PGPB-synthesizing IAA may prevent the deleterious effects of environmental stresses (Lindberg et al. 1985; Frankenberger and Arshad 1995). For example, IAA stimulated lengthening of the root and shoot of wheat seedling exposed to high levels of saline (Egamberdieva 2009). An increased tolerance of *Medicago truncatula* against salt stress was also observed in plants nodulated 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.

On the other hand, IAA is a readily biodegradable compound and bacteria able to catabolize IAA have been recovered from various environments, including soil (Gieg et al. 1996) and plant tissues (Libbert and Risch 1969; Strzelczyk et al. 1973; Leveau and Lindow 2005). Degradation of IAA has been reported for strains belonging to *Pseudomonas* (Gieg et al. 1996; Leveau and Lindow 2005), *Arthrobacter* (Mino 1970), *Alcaligenes* (Claus and Kutzner 1983) and *Bradyrhizobium* (Jensen et al. 1995; Jarabo-Lorenzo et al. 1998) genera. Recently, the *iac* locus a cluster of ten genes for the catabolism of IAA that showed some similarity to genes encoding enzymes that catabolized indole or amidated aromatics, was detected in *P. putida* 1290 (Leveau and Gerards 2008). In this regard, degradation of IAA, or its inactivation, provides bacteria with the potential for manipulation of the plant's IAA pool and its related impact on plant physiology and growth.

### 2.3.2 Cytokinins and Gibberellins

Cytokinins are N6-substituted aminopurines that play a key role in a wide range of physiological processes such as plant cell division, interruption of the quiescence of dormant buds, activation of seed germination, promotion of branching, root growth, accumulation of chlorophyll, leaf expansion, and delay of senescence (Salisbury and Ross 1992). In addition, cytokinins regulate the expression of the gene coding for expansin, a protein that induces the loosening of plant cell walls and thereby facilitates turgor-driven plant cell expansion, which affects both the size and the shape of the cells (Downes and Crowell 1998; Downes et al. 2001).

The gene encoding the enzyme responsible for the synthesis of cytokinins was initially characterized in *Agrobacterium tumefaciens* (Nester et al. 1984) and subsequently found in methylotrophic and methanotrophic bacteria (Koenig et al. 2002; Ivanova et al. 2001). Since then, many PGPB including *Azotobacter*,

*Azospirillum*, *Rhizobium*, *Bacillus*, and *Pseudomonas* spp., have been found to produce this hormone (Nieto and Frankenberger 1989; Timmusk et al. 1999; Salamone et al. 2001; Taller and Wong 1989).

Interestingly, unlike the situation in bacteria, the gene encoding isopentenyl-transferase, the cytokinin biosynthesis enzyme, was not definitively identified in plants until 2001 (Kakimoto 2001), putting an end to speculation regarding the supposed inability of plants to produce cytokinins.

Seed inoculation with cytokinin-producing bacteria usually leads to a higher cytokinin content in the plants, with a concomitant influence on plant growth and development (Arkhipova et al. 2005). Various environmental stresses such as drought may also cause plant cytokinin levels to become elevated (Arkhipova et al. 2007), often inducing an increase in plant ethylene levels which in turn inhibits root elongation (Werner et al. 2003).

A positive correlation has been observed in several legume species between the level of cytokinins in plants and the ability of *Rhizobia* to form nodules on the roots of those plants (Yahalom et al. 1990; Hirsch and Fang 1994; Lorteau et al. 2001). In addition, cytokinins are believed to be involved in rhizobial infection and nodule differentiation (Frugier et al. 2008). A strain of *Rhizobium* sp., impaired in the synthesis of the Nod factor (Nod<sup>−</sup>) and therefore unable to nodulate its legume host, but genetically modified for the production of the cytokinin transzeatin, induced the formation, on *Medicago sativa* roots, of a nodule-like structure which remained uncolonized by *Rhizobia*, suggesting that cytokinins can mimic some of the morphogenetic effects of Nod factors.

Recently, the role that cytokinin receptors play in plant growth stimulation by cytokinin-producing PGPB was elaborated. Plant growth promotion and modification of root architecture with the development of short tap roots and highly branched lateral roots with long root hairs were induced by *Bacillus megaterium* UMCV1 on *A. thaliana*; effects that were all ascribed to cytokinin synthesis, independent of auxin and ethylene signaling (Ortiz-Castro et al. 2008). Since a number of PGPB that synthesize cytokinins stimulate the growth of different crops, it's likely that this plant beneficial activity is mediated by different cytokinin receptor homologs (Ortiz-Castro et al. 2008).

Gibberellins are synthesized by higher plants, fungi, and bacteria; they are diterpenoid acids consisting of isoprene residues (generally with four rings); to date 136 different gibberellins have been identified and characterized (MacMillan 2002). They affect cell division and elongation and are involved in several plant developmental processes, including seed germination, stem elongation, flowering, fruit setting, and delay of senescence in many organs of a range of plant species (MacMillan 2002). Gibberellins have also been implicated in promotion of root growth since they regulate root hair abundance (Bottini et al. 2004). However, in these processes gibberellins interact with other phytohormones and alter the plant's hormonal balance thereby affecting plant growth (Trewavas 2000).

The ability of bacteria to synthesize gibberellins-like substances was first described in *Azospirillum brasilense* (Tien et al. 1979) and *Rhizobium* (Williams and Sicardi de Mallorca 1982); it has since been detected in different bacterial

genera that inhabit the plant root system including *Azotobacter*, *Arthrobacter*, *Azospirillum*, *Pseudomonas*, *Bacillus*, *Acinetobacter*, *Flavobacterium*, *Micrococcus*, *Agrobacterium*, *Clostridium*, *Rhizobium*, *Burkholderia*, and *Xanthomonas* (Mitter et al. 2002; Tsakelova et al. 2006; Joo et al. 2009). Plant growth promotion by gibberellin-producing PGPB has been reported by several labs, and this positive effect on plant biomass is frequently associated with an increased content of gibberellins in plant tissues (Atzhorn et al. 1988; Gutierrez-Manero et al. 2001; Joo et al. 2005, 2009; Kang et al. 2009). Modification of the gibberellin concentration in plants is the result of either (a) gibberellin synthesis (Lucangeli and Bottini 1997; Piccoli et al. 1999), (b) deconjugation of glucosylgibberellins (Piccoli et al. 1997), or (c) chemical activation of inactive gibberellins by PGPB (Cassán et al. 2001a, b).

*Azospirillum* spp. is a nitrogen fixing and IAA-producing PGPB that is well known to induce enhancement of plant growth and yield (Okon and Labandera-Gonzalez 1994) under both nonstressed as well as stressful conditions such as drought (Creus et al. 1997). Besides improving N nutrition under some conditions, plant growth promotion activity by *Azospirillum* spp. may also be related to gibberellin synthesis. Moreover, the capability to deconjugate the conjugated form of gibberellins or to activate inactive forms of gibberellins has been implicated in plant growth promotion and reversal of dwarf phenotype in rice and maize, which lack the ability to synthesize gibberellin, by *A. lipoferum* and *A. brasilense* (Lucangeli and Bottini 1997; Cassán et al. 2001a, b).

### 2.3.3 Ethylene

The synthesis of ethylene in all higher plants is based on three enzymes (a) S-adenosyl-L-methionine (SAM) synthetase, which catalyzes the conversion of methionine to SAM (Giovanelli et al. 1980), (b) 1-aminocyclopropane-1-carboxylic acid (ACC) synthase, which mediates the hydrolysis of SAM to ACC and 5'-methylthioadenosine (Kende 1989), and (c) ACC oxidase which metabolizes ACC to ethylene, carbon dioxide, and cyanide (John 1991). Although several phases of plant growth (i.e., fruit ripening, flower senescence, leaf and petal abscission) are regulated by ethylene, this phytohormone is also important for its role in plant responses to biotic and abiotic stresses (Abeles et al. 1992). The term "stress ethylene" (Abeles 1973), describes the increase in ethylene synthesis associated with environmental stresses including extremes of temperature, high light, flooding, drought, the presence of toxic metals and organic pollutants, radiation, wounding, insect predation, high salt, and various pathogens including viruses, bacteria, and fungi (Morgan and Drew 1997).

The increased level of ethylene formed in response to environmental stresses can exacerbate symptoms of stress or it can lead to responses that enhance plant survival under adverse conditions. Thus, stress ethylene has been suggested to both alleviate and exacerbate some of the effects of the stress, depending upon the plant



species, its age and the nature of the stress (Van Loon and Glick 2004). This behavior is explained by a two-phase model (Glick et al. 2007). When plants are exposed to stress, they quickly respond with a small peak of ethylene that initiates a protective response by the plant, such as transcription of pathogenesis-related genes and induction of acquired resistance (Ciardi et al. 2000; Van Loon and Glick 2004). If the stress is chronic or intense, a second much larger peak of ethylene occurs, often 1–3 days later. This second ethylene peak induces processes such as senescence, chlorosis, and abscission that may lead to a significant inhibition of plant growth and survival.

In 1978, an enzyme capable of degrading the ethylene precursor, ACC, to ammonia and  $\alpha$ -ketobutyrate was isolated from *Pseudomonas* sp. strain ACP (Honma and Shimomura 1978). Further studies demonstrated the presence of ACC deaminase activity in a wide range of soil microorganisms including the fungus *Penicillium citrinum* (Honma 1993), and various bacteria (Jacobson et al. 1994; Glick et al. 1995; Burd et al. 1998; Belimov et al. 2001; Ma et al. 2003; Ghosh et al. 2003; Sessitsch et al. 2005; Blaha et al. 2006; Madhaiyan et al. 2007; Kuffner et al. 2008; Chinnadurai et al. 2009). Bacterial ACC deaminase activity is relatively common. In one study, 12% of isolated *Rhizobium* spp. from various sites in southern and central Saskatchewan possessed this enzyme (Duan et al. 2009). In another study, ACC deaminase activity/genes were found in a wide range of bacterial isolates including *Azospirillum*, *Rhizobium*, *Agrobacterium*, *Achromobacter*, *Burkholderia*, *Ralstonia*, *Pseudomonas*, and *Enterobacter* (Blaha et al. 2006).

In a model described by Glick et al. (1998), PGPB colonize the seed or root of a developing plant and, in response to tryptophan and other small molecules in seed or root exudates (Bayliss et al. 1997; Penrose and Glick 2001), the bacteria synthesize and secrete IAA (Patten and Glick 1996, 2002). This IAA, and the endogenous plant IAA, can either stimulate plant growth or induce the synthesis of ACC synthase, which converts SAM to ACC. A portion of the ACC produced by this reaction is exuded from seeds or plant roots (Bayliss et al. 1997; Penrose and Glick 2001), taken up by the bacteria, and converted by ACC deaminase to ammonia and  $\alpha$ -ketobutyrate. As a result of this activity, the amount of ethylene produced by the plant is reduced. Therefore, root colonization by bacteria that synthesize ACC deaminase prevents limits ethylene levels that might otherwise be growth inhibitory (Glick 1995). The main visible effect of seed inoculation with ACC deaminase-producing bacteria, under gnotobiotic conditions, is the enhancement of root elongation (Glick et al. 1995; Hall et al. 1996; Shah et al. 1997).

In addition, other processes such as nodulation of legumes and mycorrhizal establishment in the host plant induce local increases in ethylene content. In this context, ACC deaminase-producing bacteria, lowering the ethylene content in the plants, can increase both nodulation and mycorrhizal colonization in pea (Ma et al. 2003) and cucumber (Gamalero et al. 2008), respectively.

Bacteria that have ACC deaminase facilitate plant growth under a variety of ethylene-producing environmental stresses including flooding (Grichko and Glick 2001; Farwell et al. 2007), pollution by organic toxicants such as polycyclic-aromatic hydrocarbons, polycyclic biphenyls, and total petroleum hydrocarbons



(Saleh et al. 2004; Huang et al. 2004a, b; Reed and Glick 2005) and by heavy metals including nickel, lead, zinc, copper, cadmium, cobalt, and arsenic (Burd et al. 1998, 2000; Belimov et al. 2001, 2005; Nie et al. 2002; Glick 2003; Reed and Glick 2005; Farwell et al. 2006; Rodriguez et al. 2008), salinity (Mayak et al. 2004b; Saravanakumar and Samiyappan 2006; Cheng et al. 2007; Gamalero et al. 2009), drought (Mayak et al. 2004a), and phytopathogen attack (Wang et al. 2000; Hao et al. 2007).

## 2.4 Soil-borne Disease Suppression

Plant disease suppression by soil microorganisms is a possible alternative means of reducing the chemical input in agriculture (Compant et al. 2005). Biocontrol of plant pathogenic microorganisms relies on different traits including competition for colonization site or nutrients, production of antibiotics and enzymes, and induction of systemic resistance (ISR) against the pathogens (Raaijmakers et al. 2009).

Competitive colonization of the root system and successful establishment in the zones of the roots that are preferentially colonized by the pathogen is a prerequisite for effective biocontrol (Weller 1988; Raaijmakers et al. 1995). In addition, the synthesis of several antagonistic molecules through quorum sensing is directly linked to the proliferation of the PGPB on the roots. Moreover, PGPB can outcompete some pathogens by degrading organic compounds or sequestering micronutrients (i.e., iron), which are also required for the growth and the development of deleterious microorganisms (Fravel et al. 2003; Lemanceau et al. 1992).

A number of factors such as soil composition, temperature, relative humidity, composition of root exudates, presence of recombinant plasmids as well as the interactions with other soil biota can affect the persistence of a PGPB on the root system making it difficult to predict the behavior of the bacterial strain under natural conditions. Therefore, PGPB that are effective in the laboratory frequently do not show any significant impact on plants in the field (Glick et al. 1999).

The synthesis of antibiotics is the mechanism that is most commonly associated with the ability of a PGPB to suppress pathogen development (Haas and Keel 2003; Whipps 2001; Mazurier et al. 2009). The antibiotics synthesized by PGPB include agrocin 84, agrocin 434, herbicolin, 2,4-diacetylphloroglucinol, oomycin, cyclic lipopeptides, hydrogen cyanide, phenazines, pyoluteorin, and pyrrolnitrin. Although the main target of these antibiotics are the electron transport chain (phenazines, pyrrolnitrin), metalloenzymes such as copper-containing cytochrome c oxidases (hydrogen cyanide), membrane integrity (biosurfactants), or cell membrane and zoospores (2,4-diacetylphloroglucinol, DAPG, biosurfactants) (Haas and Défago 2005; Raaijmakers et al. 2006) their mode of action are still largely unknown.

Other PGPB behave as biocontrol agents by producing enzymes such as chitinase, cellulase,  $\beta$ -1,3 glucanase, protease, or lipase, that induce lysis of fungal cell walls (Chet and Inbar 1994). In particular, chitinase is considered crucial for the

biocontrol activity exhibited by PGPB against phytopathogenic fungi such as *Botrytis cinerea* (Frankowski et al. 2001), *Sclerotium rolfsii* (Ordentlich et al. 1988), *Fusarium oxysporum* f.sp. *cucumerinum* (Singh et al. 1999) and *Phytophthora* (Kim et al. 2008) and  $\beta$ -glucanase for the suppression of *R. solani*, and *Pythium ultimum* cell walls (Frankowski et al. 2001; Ordentlich et al. 1988).

Some PGPB can trigger the phenomenon of induced systemic resistance (ISR) which is phenotypically similar to systemic acquired resistance (SAR) which occurs when plants activate their defense mechanism in response to primary infection by a pathogen. ISR involves jasmonate and ethylene signaling within the plant that stimulates the host plant's response to a range of pathogens without requiring direct interaction between the resistance-inducing microorganisms and the pathogen (Bakker et al. 2007). Besides ethylene and jasmonate, other bacterial molecules such as the *O*-antigenic side chain of the bacterial outer membrane protein lipopolysaccharide (Leeman et al. 1995), flagellar fractions (Zipfel et al. 2004), pyoverdine (Maurhofer et al. 1994), DAPG (Iavicoli et al. 2003; Siddiqui and Shoukat 2003), cyclic lipopeptide surfactants (Ongena et al. 2007; Tran et al. 2007) and, in some instances, salicylic acid (van Loon et al. 1998) have been implicated as signals for the induction of systemic resistance.

Most studies of systemic resistance have been carried out using fungal pathogens; however, this approach may also have potential in the control of bacterial pathogens such as *P. syringae* pv. *lachrymans*, the causal agent of bacterial angular leaf spot (Liu et al. 1995). ISR can induce alterations to host physiology leading to an overexpression of plant defensive chemicals including pathogenesis-related proteins such as chitinases, peroxidases, superoxide dismutase phenylalanine ammonia lyase, phytoalexins, and polyphenol oxidase enzymes (Bakker et al. 2007).

Using genetic engineering techniques, it should be possible to create superior biocontrol strains that utilize two or more different mechanisms to protect plants against phytopathogens. For example, genes encoding enzymes such as chitinase may readily be expressed in biocontrol bacteria that produce specific antibiotics. Moreover, the efficacy of any biocontrol strain may be improved by the introduction of an ACC deaminase gene (Wang et al. 2000; Hao et al. 2007).

## 2.5 Conclusions

In the past 10–15 years, there has been an increasing interest in the possibility of utilizing PGPB as adjuncts to agricultural and horticultural practice as well as environmental cleanup. Moreover, with this interest there has been a major effort worldwide to better understand many of the fundamental mechanisms that PGPB use to facilitate plant growth. These basic studies are predicated on the notion that it is necessary to first understand the fundamental genetic and biochemical mechanisms that govern the relationship between PGPB and plants before using them on a massive scale in the environment. With increasing concern about the natural environment and the understanding that the era of the large scale use of

chemicals in the environment needs to come to an end, PGPB offer an attractive alternative that contains the possibility of developing more sustainable approaches to agriculture. Finally, it is likely to be much simpler and more efficacious to select or engineer PGPB so that they confer plants with specific desirable traits than to genetically engineer the plants themselves to the same end.

**Acknowledgments** The work from our laboratories that is cited here was supported by funds from the Italian Ministry of Education, University and Research and the Natural Sciences and Engineering Research Council of Canada.

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Bacteria in Agrobiolology: Plant Nutrient Management

Maheshwari, D.K. (Ed.)

2011, XII, 345 p., Hardcover

ISBN: 978-3-642-21060-0