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Volume-2: Applications of Microbes for Sustainable Agriculture and in-silico Strategies

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Contents

Plant Growth-Promoting Rhizobacteria for Sustainable Agriculture

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Abstract

Plant growth-promoting rhizobacteria (PGPR) are closely allied with roots and can improve plant growth and inhibit the invading pathogens. The PGPR stimulates plant growth by various means, viz., increased nutrient uptake and production of hormones (IAA, gibberellins, cytokinins, etc.) and bioactive substances (to antagonize phytopathogenic microbes) along with the synthesis of enzymes that regulates plant ethylene levels. Recently, PGPR has attracted many researchers' attention to the development of biofertilizers as an eco-friendly approach. However, potential PGPR selection is an important factor, as plants' responses to environmental conditions often vary based on plant genotype, experimental sites, and seasons. A PGPR isolated from the native crop plants or their ecological zone is considered productive and efficient with steady results if reused at the same site and crop. Extensive studies have suggested that PGPR could have emerged as a promising and substitute chemical fertilizer method for agriculture sustainability. With this background, the interactions involving PGPR populations with plants are the current challenge to explore their use under various agroclimatic conditions. The diverse group of PGPR isolated from various plants' rhizosphere and their role in increasing soil fertility, stress management, bioremediation, etc. are reviewed and discussed in this chapter.

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1.1 Introduction

The rhizosphere zone consists of numerous microorganisms and the zone itself influences plants the most due to numerous activities in the roots (Uren 2000). The term "rhizosphere" was defined first as "the soil compartment affected by the plant root" by Lorenz Hiltner, the German agronomist, in 1904. The plant's rhizosphere is a zone of exceptional microbial action and a few microorganisms are bounteously present in this zone, named rhizobacteria, and have shown their various capacities. The nutrients do not just profit a portion of these rhizobacteria (as supplements) secreted by the plant root yet gainfully impact plant growth through different phenomena (Gowtham et al. 2018; Hariprasad et al. 2021).

1.1.1 Plant Growth-Promoting Rhizobacteria (PGPR)

The bacteria that colonize the host plant's roots and enhance its growth are generally termed as plant growth-promoting rhizobacteria (PGPR) (Gowtham et al. 2018). They are utilized as biofertilizers, biopesticides, bio-herbicides, and biocontrol agents (Hariprasad et al. 2021). The study of PGPR's interactions with plants and other microorganisms is often complicated in their biotic environment. These bacteria are classified based on their beneficial traits as biofertilizers capable of nitrogen fixation. The phyto-stimulators with the aptitude to produce hormones may act as biocontrol agents to protect plants from phytopathogenic microbe infection. The use of PGPR as bio-inoculants on crops would be a cost-effective biological disease management technique. It reduces the usage of chemical fertilizers, which also pollutes the atmosphere and causes human health problems (Gowtham et al. 2020). Furthermore, PGPR use will assist in increasing crop production, thereby helping to feed the mounting population. For three decades, a variety of PGPR (such as *Bacillus*, *Pseudomonas*, *Burkholderia*, *Enterobacter*, *Azotobacter*, *Azospirillum*, *Serratia*) have been documented to suppress a variety of fungal diseases while also significantly improving seed germination, root growth, and plant water uptake (Akhtar and Siddiqui 2010).

1.1.2 Diversity of the PGPR

The rhizobacterial diversity has been studied to a greater extent in numerous crops and other organisms, with the release of plant growth promoters (auxin, cytokinin, gibberellin, jasmonic acid, salicylic acid, abscisic acid, and ethylene), antagonistic metabolites (siderophores, antibiotics, hydrogen cyanide), soil enzymes (urease,

proteases, dehydrogenase, nitrogenase, phosphatase), and inducers of systemic disease resistance (ISR) being used to assess their functionality (Johri et al. 2003). Scientists have been researching the accessibility of modern tools to study the microbial communities allied for improved plant growth for over a century. Structural and functional diversity are two approaches to studying the bacterial population. To comprehend the systemic approach, we must first understand the classes of individuals, their organisms, and their abundance.

The functional diversity of rhizobacteria is also explored through the screening of beneficial traits in rhizobacteria. Since the culture-based methods cannot isolate unculturable bacteria, they may not be appropriate for studying soil bacterial diversity (Amann et al. 1995). Denaturing gradient gel electrophoresis (DGGE) is an imperative method for studying bacterial population diversity and dynamics (Muyzer and Ramsing 1995). Muyzer et al. (1993) introduced DGGE of polymerase chain reaction (PCR)-amplified rDNA (ribosomal DNA) fragmented into microbial ecology and used it to research the genetic diversity of microbes from a variety of environments to examine the rhizobacterial population using molecular techniques. The analysis used by Muyzer et al. (1995) provided information on the genetic diversity of microbial communities located around the hydrothermal vents. Different isolation and purification methods yielded distinct PCR-DGGE profiles in rhizosphere samples, which reflected different bacterial consortia (Niemi et al. 2001). Gelsomino et al. (1999) have also used PCR and DGGE analysis to establish the bacterial population structure in Flevo silt loam soil. By examining the amplification, they showed that the species of *Arthrobacter* and *Enterobacter* were dominant in soil. Griffiths et al. (2000) used DGGE microbial population analysis to discern the active portion (rRNA derived) from total bacterial diversity (rDNA derived) across horizons of an existing grassland soil. DGGE of PCR and reverse transcriptase (RT) PCR-amplified 16S rRNA was used to investigate the rhizosphere-resident bacterial communities of *Chrysanthemum* (*Dendranthema grandiflora* Tzvelev) that majorly consisted of previously mentioned soil bacteria (*Pseudomonas*, *Acetobacter*, *Bacillus,* and *Arthrobacter*) (Duineveld et al. 2001).

Fang et al. (2005) used PCR amplification and DGGE analyses to assess the bacterial diversity in transgenic and non-transgenic corn rhizospheres and confirmed that the diversity of bacteria did not vary among the evaluated samples. Costa et al. (2006) have used DGGE to investigate the rhizosphere-resident bacteria of *Brassica napus* L. and *Fragaria ananassa* and found that *Streptomyces* and *Rhizobium* species were dominant ribotypes in the *F. ananassa* rhizosphere. At the same time, *Arthrobacter* sp. was the dominant ribotype in the *B. napus*, according to DGGE bands found in the bacterial profiles. Brons and van Elsas (2008) used PCR-DGGE fingerprinting and cluster analysis to determine the soil bacterial population's composition. Besides, Monteiro et al. (2009) investigated the bacterial communities of the rhizospheres of three different genotypes of Vetiver [*Chrysopogon zizanioides* (L.) Roberty] and found that the predominant rhizospheric bacterial community hardly differs depending on the Vetiver genotype, according to the DGGE profiles.

PCR-DGGE was used by Yuan et al. (2010) to investigate the divergence in rhizobacterial communities of *Fritillaria thunbergii* grown in different habitats. The bacterial diversity was determined using principal component analysis (PCA), which revealed significant differences between all the soil samples collected from various habitats. Also, the same technique was used to examine the diversity of bacteria from the rhizosphere of *Colobanthus quitensis* (Kunth) Bartl and *Deschampsia antarctica* É. Desv (Teixeira et al. 2010). The Pearson's correlation index revealed no specific cluster formation irrespective of sample sites with >90% similarity. The DGGE was used by Nimnoi et al. (2011) to investigate the effects of rhizobial inoculants of three plants which revealed distinct communities of rhizobacteria on the created dendrogram and Sorensen's index. The findings indicated that the host and its rhizosphere soil had a synergistic impact on rhizobacterial communities. They also discovered that the inoculants played a role in the rhizosphere group structure changes. According to the hierarchical cluster analysis, the population structure of *D. elliptica* was more different from that of the other plants evaluated. The culture-dependent and -independent methods were used to examine the diversity of bacteria associated with maize roots by Pereira et al. (2011). Firmicutes, predominantly of the *Bacillus* genus, were found in abundance combined with the roots using culturable methods, while the genera of *Achromobacter*, *Lysinibacillus*, and *Paenibacillus* were found infrequently.

For analyzing the actinobacterial diversity of Panxi and China, the researchers combined culture-dependent and -independent methods from seven medicinal plants' rhizosphere (Zhao et al. 2012). The amplification of V6–V8 regions of 16S rDNA sequence revealed that *Agrobacterium*, *Burkholderia*, *Enterobacter*, and *Pseudomonas* genera were abundant in the rhizosphere soil of canola (Farina et al. 2012). Several of these bacteria have been shown to produce IAA and siderophores, solubilize phosphate, fix nitrogen, and promote canola plant growth. The DGGE analysis on *Eucalyptus globulus* callus and stem base's superficial tissues revealed that the bacterial populations differed at different sampling times (Peralta et al. 2012).

The examination of pearl millet rhizosphere of Faridabad, India, revealed *Bacillus*, *Flavobacterium*, *Pseudomonas*, *Staphylococcus*, *Streptococcus*, and *Streptomyces* as dominant bacterial isolates (Prashar et al. 2012). Simpson index (D), Shannon-Wiener index, and equitability were determined to be 0.81, 1.71, and 0.95, respectively. Under in vitro conditions, the isolates were found to produce HCN, IAA, and ammonia along with the ability to solubilize phosphate. The isolates from the genus *Pseudomonas* had the greatest potential for promoting plant growth, whereas those from the genera *Staphylococcus* and *Streptomyces* had the least. Likewise, Gaikwad and Sapre (2015) investigated the rhizobacterial diversity in plant roots cultivated in the Solapur district, Maharashtra, India. They found that the structural diversity reported was the highest in the coriander rhizosphere, which was supported by its higher Simpson index value. When bacterial isolates from coriander and turmeric were compared to bacterial isolates from other plants, the functional diversity, assessed based on their PGPR traits and efficiency in controlling the growth of phytopathogen (*Sclerotium rolfsii*), revealed that the bacterial isolates

produced IAA, siderophore, and HCN, and also possessed the ability to solubilize phosphate and chitin.

1.2 Mechanism of Actions of PGPR for Plant Growth Promotion and Disease Suppression

Use of biological agents, such as PGPR, is one of the most recent ways to counteract biotic and abiotic stresses' negative effects. PGPR are rhizosphere-competent bacteria that colonize and multiply on plant roots irrespective of their growth stage (Antoun and Kloepper 2001). Rhizobacteria serve as eco-friendly and sustainable alternatives to the unsafe chemicals used for growth promotion and control of plant diseases (Shankar et al. 2009). The PGPR strains used as fresh suspensions and powdered formulations have commercial potential in plant growth promotion and management of plant diseases as evident from several researchers (Chithrashree et al. 2011). The PGPR usage in agriculture will boost plants' growth under stress conditions (Dimkpa et al. 2009) and decrease chemical fertilizers' usage. The mechanisms underlying the PGPR-mediated growth promotion in many crop plants are still unclear but some mechanisms identified include solubilization of minerals, root colonization and competition, nitrogen fixation, ability to synthesize phytohormones, and antagonism against phytopathogens through the production of siderophores, antibiotics, cyanide, chitinases, and β-1,3-glucanase along with the ability to synthesize enzymes that regulates plant ethylene levels and hydrolytic enzymes (Fig. 1.1) (Gupta et al. 2015; Hariprasad et al. 2021).

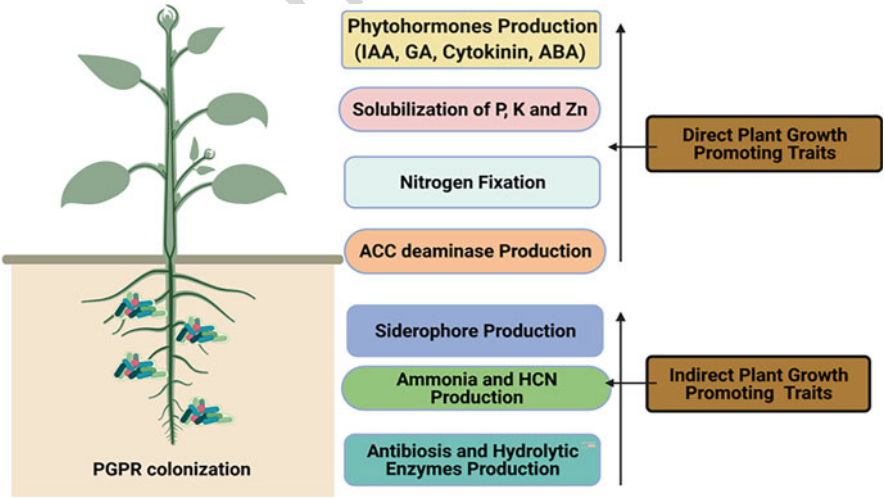

Fig. 1.1 Schematic representation of direct and indirect mechanisms of PGPR for plant growth

1.2.1 Root Colonization and Competition

Bacterial cells form a colony on the root's surface and further a biofilm made up of an extracellular polysaccharide matrix. The steps in root colonization include initial attachment, colony formation, and maturation of biofilm and it is necessary for its beneficial nature and to understand the mechanisms involved (Nayak et al. 2020). Microorganisms, including fungi, bacteria, protozoans, and nematodes, are all known to be inhibited or stimulated by the root's unidentified compounds. Further studies by Paterson et al. (1993) revealed that soil density, water-holding ability, and other factors influenced root colonization significantly. Similar experiments conducted by Beauchamp et al. (1993) in the rhizosphere soil of potato revealed the colonization of bacteria up to 8 cm length of roots at high temperatures. In addition to these factors, quorum sensing plays a significant part in finding out the root-colonizing bacterial density in the rhizosphere (Pierson et al. 1998). According to Gamalero et al. (2004), there was no major temporal difference in the density of total bacterial cells in any of the root zones examined. The microscopic analysis results revealed that all zones had a similar bacterial cell distribution pattern with lower density initially. But in later stages, zone A had the same pattern of colonization. Still, in contrast, zones B and C, which had root colonization to higher densities, thereby depicting the spatial pattern of colonization, were related to the differentiation in root zones.

To screen root-colonizing bacteria, Silva et al. (2003) established a simple root colonization bioassay. The bacteria that colonized roots in repeated experiments were considered positive for root colonization. The bacterized seeds were placed on 0.6 g of water agar and observed for the opaque zone around the growing roots. Mafia et al. (2009) used the same approach to screen root-colonizing bacteria in *Eucalyptus* seedlings. Apart from root colonization, PGPR must contend with native microbes for nutrients within the rhizosphere if pathogens can be successfully eliminated. Rhizobacteria that promote plant growth also battle with pathogens for nutrients in root exudates and eventually outnumbering them. PGPR populations on plant roots can serve as a sink for available nutrients, limiting the amount of nutrients available for invading pathogens (Bashan and de-Bashan 2005).

Biocontrol rhizosphere bacteria can multiply and spread throughout the rhizosphere system, colonizing possible infection sites on the root, thereby competing directly with the pathogens, including antibiotic production (Yasmin et al. 2009), siderophore (Singh et al. 2019), hydrolytic enzymes (Ramos-Solano et al. 2010), and fungal pathogen inhibition by hyphal colonization (Yang et al. 1994) and ISR (Fig. 1.2) (Gowtham et al. 2018). The colonization ability of PGPR to an acceptable density is required for successful biological control, but it is necessary to track its ability to colonize the root to screen an efficient root colonizer. Since tracking bacteria introduced into complex environments like soil necessitates the ability to distinguish them from native microflora, the markers used for this reason must meet certain criteria.

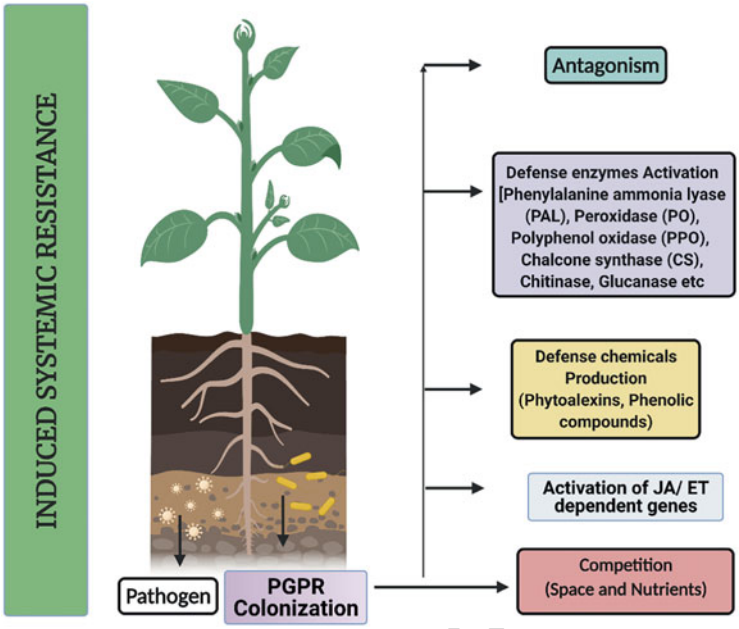

Fig. 1.2 Mode of induction of systemic resistance to various diseases

1.2.2 Nitrogen Fixation

For plant growth, nitrogen is the most limiting nutrient, and to fix this nitrogen for accessibility to plants, a specific microbe group is needed. Biological nitrogen fixers are microorganisms that fix nitrogen in the environment. They convert inert N_2 into a plant-friendly organic form (Reed et al. 2011). N_2 fixation accounts for up to 25% of total nitrogen in plants. Plant roots discharge substances that encourage colonization of bacteria and fix nitrogen, thereby effectively substituting the chemical fertilizers in various ways in dropping the environmental pollution. Even though many N_2-fixing bacteria are associated with legumes, members of the *Azotobacter* and *Azospirillum* genera have been extensively experienced in the field to increase legume and cereal yields (Nosheen et al. 2021).

The most common species present in the soil is *Azotobacter chroococcum*, but other species such as *A. beijerinckii*, *A. insignis*, *A. macrocytogenes*, and *A. vinelandii* can also be found (Kizilkaya 2009). The association of *A. chroococcum* in rhizospheres of plants was linked to increased seedling growth and germination (Sumbul et al. 2020). The presence of low levels of organic matter in soils is a significant limiting factor for *Azotobacter* proliferation; as a result, the rhizoplane is devoid of *Azotobacter* cells (Sammauria et al. 2020). *Azospirillum* mostly forms a symbiotic relationship with the plants to increase crop yield. It was shown that inoculating the plant with both *Azospirillum lipoferum* and *Bacillus megaterium*

provided balanced nitrogen nutrition and resulted in an enhanced crop yield than inoculating the wheat plant with only *Azospirillum* (El-Komy 2005).

1.2.3 Phosphate Solubilization

Phosphorus is the second important nutrient for plants. Even though total phosphorous levels in soils are typically high and most of them are insoluble, some emerge after applying chemical fertilizers (Penn and Camberato 2019). Microorganisms were believed to be involved in the solubilization of inorganic phosphates as early as 1903. Phosphate-solubilizing microbes are found everywhere, but their numbers differ from one soil to the next. The phosphate-solubilizing bacteria make up 50% of the soil's total population, while fungi make up 0.5–1%. Phosphate-solubilizing bacteria outnumber phosphate-solubilizing fungi by a factor of 2–150 (Khan et al. 2007). The phosphate-solubilizing microbes make up 40% of the culturable population which are largely isolated from rhizosphere soil (Sharma et al. 2013). The majority of phosphate-solubilizing bacteria have been isolated from the rhizospheric soil of different plants. They are metabolically more active than the bacteria that possess phosphate-solubilizing ability from different sources (Vazquez et al. 2000). Mineral phosphate solubilization is the mechanism of converting the insoluble form of phosphorus into soluble mono- and dibasic phosphate ions. As a result, phosphorus supply to plants increases (Gyaneshwar et al. 2002; Penn and Camberato 2019).

Similarly, Islam et al. (2007) revealed that some rhizobacteria isolated from the rice-grown soil were found to be phosphate solubilizers. Since they observed a decrease in pH of the culture and bacterial growth due to the accumulation of organic acids, phosphate solubilization was reported as supportive for organic acid production. Besides, these organisms boost the efficacy of nitrogen fixation and increase the availability of trace elements like Fe, Zn, and others (Nosheen et al. 2021). Khan and Khan (2001) demonstrated the management of wilt disease caused by *Fusarium* in tomato under field trials by applying phosphate-solubilizing microbes to the soil. Following soil application in the field, these phosphate solubilizers significantly increased vegetative and reproductive growth parameters. Certain PSM also reduced *Fusarium* incidence, which is linked to a lower *F. oxysporum* in the rhizosphere.

Dey et al. (2004) examined bacterial isolates from nine soil samples; eight produced siderophores and five produced IAA. Soilborne fungal pathogens like *Sclerotium rolfsii* were inhibited by ammonia and solubilized inorganic phosphate. The efficiency of these rhizobacterial isolates was tested in pot and field trials for 3 years. In both rainy and post-rain seasons, phosphate content in soil, shoots, and kernels increased significantly after bacterial inoculation. Similarly, Han et al. (2006) used phosphate- and potassium-solubilizing rhizobacteria to increase the nutrient availability and uptake capacity of pepper and cucumber in their experiment. Compared to other combinations, rock phosphate and rock potassium and co-inoculation improved the accessible P and K in potting medium significantly. The same combination increased pepper and cucumber plants' NPK content in shoots and roots and their dry weight and photosynthetic potential. Islam et al.

(2007) isolated phosphate-solubilizing bacteria from a rice rhizospheric soil sample and characterized them for PGPR traits, including ammonia (NH_3) synthesis, protease, chitinase, cellulase, and β-1,3-glucanase function. According to their findings, the isolate may have more than one trait that encouraged plant growth while also suppressing plant disease.

1.3 Phytohormone Synthesis

Plant hormones are generally referred to as endogenous (naturally occurring) growth substances in plants. Auxin (indole acetic acid), gibberellins (GAs), and cytokinin (zeatin) are examples of plant growth promoters, while abscisic acid, xanthoxin, and violaxanthin are examples of plant growth inhibitors. They are usually found in plants at <1 μM and above this concentration it is considered supraoptimal (Naqvi 2002). As sessile species, plants have evolved sophisticated adaptive mechanisms to respond to abiotic stress through phytohormones' mediation (Zhang et al. 2006). According to Davies and Zhang (1991), many physiological changes are linked to changes in these plant hormones' concentrations.

1.3.1 Indole Acetic Acid (IAA)

Indole acetic acid (IAA) is a natural and physiologically most active auxin found in plants that has a beneficial effect on root development (Miransari and Smith 2014). Up to 80% of rhizobacteria can synthesize IAA and colonize seed and/or root surfaces. They work in tandem with plants' IAA to promote cell proliferation and improve the host's absorption of micronutrients (Vessey 2003). It is involved in many processes, including cell division, differentiation and extension, germination, regulation of vegetative growth, initiation of adventitious and lateral root formation, mediation of light and gravity responses, photosynthesis, metabolite biosynthesis, pigment formation, as well as tolerance to stressful situations (Spaepen and Vanderleyden 2011). The PGPR, which possesses the ability to produce IAA, has increased the growth of many crop plants (Sachdev et al. 2009; Erturk et al. 2010; Gowtham et al. 2017; Singh et al. 2019; Hariprasad et al. 2021). Peyvandia et al. (2010) evaluated the effect of IAA-producing *P. fluorescens* on root formation and root architecture of olive micro shoots by measuring the number and length of adventitious and lateral roots. They found that the amount of IAA produced by rhizobacteria was dependent on the amount of tryptophan in the media and the addition of the same to media enhanced the total number and length of adventitious and lateral roots. Bacteria may take amino acid tryptophan, a physiological precursor molecule for IAA biosynthesis, from plant root exudates (Gupta et al. 2015). The ability of PGPR for increased grain production in *Brassica* sp. was positively correlated with tryptophan-dependent auxin production (Asghar et al. 2002). Ahmad et al. (2005) isolated IAA-producing *Pseudomonas* sp. and *Azotobacter* sp. from various rhizospheric soil samples and characterized them using cultural

and biochemical characteristics and its impact on IAA production. They discovered that as tryptophan concentrations increased from 0 to 5 mg/mL, IAA production increased in both rhizobacteria genera.

1.3.2 Cytokinins

Cytokinins affect plant physiological and developmental processes as they are directly involved in cell division and growth process (Srivastava 2002). Plant growth and development can be influenced by cytokinins released by nonpathogenic microorganisms living near the roots (Garcia de Salamone et al. 2001). Also, a wild-type strain *P. fluorescens* produced more of the cytokinins isopentenyl adenosine, zeatin riboside, and dihydroxyzeatin riboside than two mutants. It was also discovered that adding the precursor adenine to G20–18 cultures increased cytokinin activity. Garcia de Salamone et al. (2001) found that mutant strains were less capable of promoting radish plant growth than wild-type strain G20–18 in previous studies.

Bacillus cereus, *B. megaterium*, *B. subtilis*, *Escherichia coli*, *Halomonas desiderata*, *Klebsiella pneumoniae*, *Proteus mirabilis*, and *Proteus vulgaris* all had phytohormones, including cytokinins, in their culture medium (Karadeniz et al. 2006). The cytokinin fractions isolated from the extract of bacteria were isolated by TLC and HPLC, according to Hussain and Hasnain (2009). In comparison to control, the bacterial extract increased cell division, cotyledon size, and fresh weight of cucumber cotyledons grown under light and dark conditions. Though the cytokinin-producing bacterial effect on plant cell division was studied primarily in the formation of root nodules (Markmann and Parniske 2009) it has been shown to promote cell division in inoculated wheat root tips (Molina-Favero et al. 2007). *Arabidopsis thaliana* mutant plants without receptors of cytokinin (*AHK2*, *AHK3*, and *CRE1*) and cytokinin signaling gene (*RPN12*) were treated with *Bacillus megaterium* to evaluate the function of cytokinin in plant growth upon treatment. The results of the study revealed that the knockout of triple-cytokinin receptors was insensitive to bacterial inoculation indicating their role in plant growth promotion (Ortiz-Castro et al. 2008). Accordingly, many PGPR have been proved to produce optimum levels of cytokinin than phytopathogens that function as inhibitors, thereby helping the plant in growth promotion (Kang et al. 2010).

1.3.3 Gibberellins (GAs)

Gibberellins (GAs) are tetracyclic diterpenoid acids that play various roles in plant development irrespective of their growth stage (Bottini et al. 2004). In the Egyptian Nile Delta, where rice has been rotated with *Trifolium alexandrinum* L. since antiquity, Yanni et al. (2001) found that indigenous *Rhizobium leguminosarum* pv. *trifolii* can colonize rice roots. *Rhizobium*-rice combination improves seedling vigor and grain yield by promoting root and shoot growth. They also discovered that *Rhizobium* formed GA, which they tentatively dubbed GA_7. In a bioassay, the dwarf

phenotype induced in alder by artificial treatment with paclobutrazol, an inhibitor of GA biosynthesis, was reversed when dwarf seedlings were treated with culture filtrate of PGPR (*Bacillus pumilus* and *B. licheniformis*) that were an inhabitant of alder rhizosphere (Gutierrez-Mannero et al. 2001). The presence of GA was discovered after GC-MS study of distilled fractions of culture filtrate. GA_1 had the highest concentration of the four types of GA detected, followed by GA_3. Probanza et al. (2002) also found that inoculating *Pinus pinea* plants with *B. licheniformis* and *B. pumilus* increased plant growth, probably through bacterial gibberellin development. *Azospirillum lipoferum* and *A. brasilense* fed with deutero GA_{20}-glycosides reversed the dwarf phenotype rice mutants, correlated with increased development (Cassan et al. 2001).

According to Joo et al. (2004), *B. cereus*, *B. macroides*, and *B. pumilus* produced GAs with the relative content of 3β-hydroxylated GAs (1, 3, 4 and 36) being higher than that of other GAs in the culture broth of the PGPR. Furthermore, Joo et al. (2005) found that using GA-producing rhizobacteria increased the fresh weight of pepper shoots and roots. It was also noted that among the three species of *Bacillus*, *B. cereus* was the most important as compared to the other two rhizobacteria as it increased the endogenous amount of GA in red pepper plants.

1.3.4 Abscisic Acid (ABA)

Abscisic acid (ABA) is one of the five "classical" plant hormones that control plant growth and development on a physiological and biochemical level (Kende and Zeevaart 1997). Abiotic stresses like salt, drought, cold, wounding, and others are directly linked to increased ABA levels (Gowtham et al. 2021). It has many effects during the plant life cycle, similar to other plant hormones. It plays a vital role in the effective alteration of plants to biotic and abiotic stresses by stomatal closure, thereby decreasing transpiration (Taiz and Zeiger 2010). The most common PGPR action mechanism to withstand stress is the induction of ABA synthesis in the plant by bacterial ABA (Cohen et al. 2001, 2009, 2015; Salomon et al. 2014). The bacterial ABA controls root elongation and architecture and water and nutrient levels and can also directly affect the concentration of hormones in the rhizosphere and leaf growth and gas exchange (Belimov et al. 2009; Dodd et al. 2010). No evidence on enhanced growth in plants is reported upon the ABA produced by the bacteria, but a few reports are available on the possible function of ABA-producing bacteria in suppressing abiotic stress in plants after bacterial inoculation. Cohen et al. (2001) showed that *Azospirillum lipoferum* inoculation partially reversed an inhibitor's effect (such as fluridone) in blocking ABA synthesis in maize seedlings and that the amount of ABA in seedlings increased and enhanced growth in comparison to fluridone treatment, thus maintaining a better water status. Cohen et al. (2008) measured the amount of ABA produced in *Arabidopsis thaliana* seedlings inoculated with the ABA-producing *Azospirillum brasilense* strain Sp245 and discovered that the ABA content was doubled when compared with uninoculated plants.

Furthermore, Cohen et al. (2009) investigated the impact of *A. lipoferum* in maize upon applying GA and ABA synthesis inhibitors, namely prohexadione-Ca and fluridone, to plants subjected to drought and adequate stress. They found that the bacterium application was as effective as that of inhibitors under both the stress conditions. Although drought-stressed plants were allowed to recover for a week, fluridone-treated and drought-stressed plants' relative water content was significantly lower, while *Azospirillum* completely nullified this impact. It was discovered to be related to ABA levels as measured by GC-EIMS. When plants were primed with only prohexadione-Ca or in combination with fluridone and subjected to drought, their growth was reduced and their ABA levels increased, implying that bacterial GAs are also essential in stress relief. The findings also indicated that both hormones released by *Azospirillum* might have helped plants cope with water stress. These findings bolstered the case for the use of beneficial bacteria with ABA-producing ability in plant stress alleviation under adverse environmental conditions. According to Salomon et al. (2014), ABA-producing *B. licheniformis* and *Pseudomonas fluorescens* increased ABA levels in 45-day-old in vitro-grown *Vitis vinifera* cv. Malbec plants by 76-fold and 40-fold, respectively, as a result of bacterization. Besides, as the amount of ABA increased, both bacteria reduced plant water loss. They hypothesized that both the bacteria serve as stress relievers by minimizing water loss and inducing ABA synthesis. Cohen et al. (2015) evaluated the morphological, physiological, and biochemical responses of *A. thaliana* Col-0 and aba2–1 mutant plants treated with ABA-producing *A. brasilense* Sp245 strain when watered and in drought stress and reported that the bacteria were effective in inducing stress tolerance.

1.3.5 Xanthoxin

Xanthoxin is an intermediate in ABA's biosynthesis and is classified as an endogenous plant growth inhibitor compared to the above five stimulatory plant hormones (Seo and Koshiba 2002). The fundamental structure and inhibitory function of xanthoxin are identical and similar to ABA (Burden et al. 1971; Taylor and Burden 1970); hence, it can be considered an ABA analog. The analog is also responsible for the stomatal closure and is found in various plant species (Raschke 1975). It is produced when violaxanthin is photooxidized and acts as an inhibitor of seed germination (Burden et al. 1971; Taylor and Burden 1972). Interestingly, Gowtham et al. (2021) confirmed the ability of *B. marisflavi* to produce ABA analog (xanthoxin-like compound) and its function in inducing drought stress tolerance in the host plant. According to their hypothesis, *B. marisflavi* catabolizes the carotenoid to produce ABA analog/xanthoxin in the rhizosphere under drought stress conditions. With the aid of xanthoxin oxidase and abscisic aldehyde oxidase, this low molecular compound (xanthoxin) can be taken up by plants, where it can either remain in its original form or be converted into ABA. Furthermore, they cause the plant to adapt physiologically to drought stress and first report ABA analog in conferring drought resistance in the host plant.

1.3.6 Ethylene

Plants can respond to any stress (both biotic and abiotic) by adjusting the level of hormones that trigger the expression of various stress-related proteins that defend plants from various negative effects of stressors (Singh et al. 2015). Ethylene is a significant plant hormone responsible for the stress response and has an important role in plant response to growth and development (Abeles et al. 1992). Plants generate the necessary amount of ethylene under ideal conditions (plant-friendly), but this amount increases when plants are exposed to stressors (adversely affect the plants) (Glick 2014). The first step in the synthesis of ethylene is converting methionine to S-adenosyl methionine, followed by 1-aminocyclopropane-1-carboxylic acid (ACC). Seedling emergence, root hair growth and elongation, tissue differentiation, lateral bud development, leaf and flower senescence, anthocyanin synthesis, fruit ripening, and processing of volatile compounds responsible for fruit fragrance are all processes in which ACC is involved (Singh et al. 2019; Gowtham et al. 2020; Hariprasad et al. 2021).

1.3.7 Production of 1-Aminocyclopropane-1-Carboxylate Deaminase

PGPR is known to support plant growth through various mechanisms, but ACC deaminase is more significant in today's environment because it protects plants from many stressors (Glick 2012). Certain plant-associated bacteria that produce ACC deaminase may minimize ethylene's stress in plants (Glick et al. 2007). ACC deaminase (EC 3.5.99.7) is a sulfhydryl multimeric enzyme with a monomeric subunit with a 35–42 kDa molecular mass. Honma and Shimomura discovered and published ACC deaminase for the first time in 1978. The enzyme ACC deaminase is located in the cytoplasm of soil bacteria and it catalyzes the conversion of ACC, an immediate precursor of ethylene, to α-ketobutyrate and ammonia, resulting in a decrease in ethylene levels in plants and the resumption of root/shoot development (Glick 2014). Induced systemic tolerance refers to the property of tolerance provided by certain bacteria to biotic or abiotic stressors by ACC deaminase activity to enhance plants' stress tolerance (Yang et al. 2009).

Among the enzymes, bacterial ACC deaminase is well known for its function in ethylene regulation that affects plants' growth and development. Rhizobacteria that produce ACC deaminase have been shown to help plants develop under abiotic stress conditions, including flooding, drought, salt, and heavy metals (Glick 2005). The increased root growth and/or enhanced development of lateral root hairs may increase tolerance to abiotic stress when the plant is inoculated with such bacteria. Rhizobacteria that develop ACC deaminase minimize ethylene's negative effects on plants caused by stress (Glick 2005). ACC deaminase producers have been identified in the bacteria *Agrobacterium*, *Bacillus*, *Burkholderia*, *Enterobacterium*, *Methylobacterium*, *Pseudomonas*, and *Rhizobium* (Penrose and Glick 2001; Pandey et al. 2005).

The decrease in ACC levels in plants caused by the ACC deaminase-synthesizing PGPR would also decrease ethylene levels, assisting the plant's growth and development (Glick 2014). According to Glick et al. (1998), PGPR with ACC deaminase activity are present at a lower level until stressors trigger it. Plant ethylene levels are dependent on the ratio of ACC oxidase to ACC deaminase, which should act before any ACC oxidase is induced since ACC oxidase has a higher affinity for ACC than ACC deaminase when PGPR with ACC deaminase is present (Glick et al. 1998). Mayak et al. (2004) found that PGPR with ACC deaminase activity endemic to rainy areas could protect plants from drought more effectively than bacteria isolated from water-rich areas. Many other researchers have confirmed the efficacy of rhizobacteria to produce ACC deaminase to protect plants against various abiotic stressors by equilibrating the amount of ethylene (Belimov et al. 2009; Gowtham et al. 2020), and the possible mechanism of action of ACC deaminase-producing PGPR is depicted in Fig. 1.3 as represented by Gowtham et al. (2020).

1.3.8 Siderophore

Iron is one of the essential micronutrients that are vital for the growth and development of plants and microbes. It has been observed that soil consists of a huge proportion of iron in its insoluble form, ferric hydroxide. The availability of iron in soil solutions is 10^{-18} M, which does not help in the sustenance of plants and can be overcome by applying microbes that can produce siderophores. Kloepper et al. (1988) were the first to discover that PGPR promotes plant growth by starving native microflora. Extracellular siderophores produced by PGPR effectively complex environmental iron, reducing its availability to certain native microflora. Many bacteria may produce multiple types of siderophores or have multiple iron-uptake systems to accommodate multiple siderophores. The species of *Bacillus*, *Serratia*, *Azotobacter*, *Pseudomonas*, *Enterobacter*, *Azospirillum*, and *Rhizobium* are only a few beneficial plant-associated bacterial genera that secrete different forms of siderophores (Ahemad and Kibret 2014). *Brucella abortus* strain 2308 is known to synthesize brucebactin (2,3-dihydroxybenzoate), a highly efficient catechol siderophore, according to Carrero et al. (2002), who used it as a siderophore for bacterial growth under iron-limited conditions. *Pseudomonas putida* DFC31 produced pyoverdine-type siderophores, and their analysis revealed the existence of hydroxymate and catecholate iron-chelating groups, according to Fu et al. (2007). The strain's IAA production and phosphate solubilization properties were also found to improve plant growth.

Helmy et al. (2008) isolated siderophores from *P. fluorescens* using affinity chromatography and identified them as 30 and 90 KDa, but they are polymers of many siderophores. *Erwinia carotovora*, the cause of bacterial soft rot in potatoes, was inhibited by a purified siderophore. The hydroxamate form of siderophores formed by *Rhizobium* isolated from *Sesbania sesban* was studied (Sridevi and Mallaiah 2008). Buyer et al. (1993) reported that PGPR produces siderophore in the rhizosphere under iron-limiting conditions using monoclonal antibodies. When

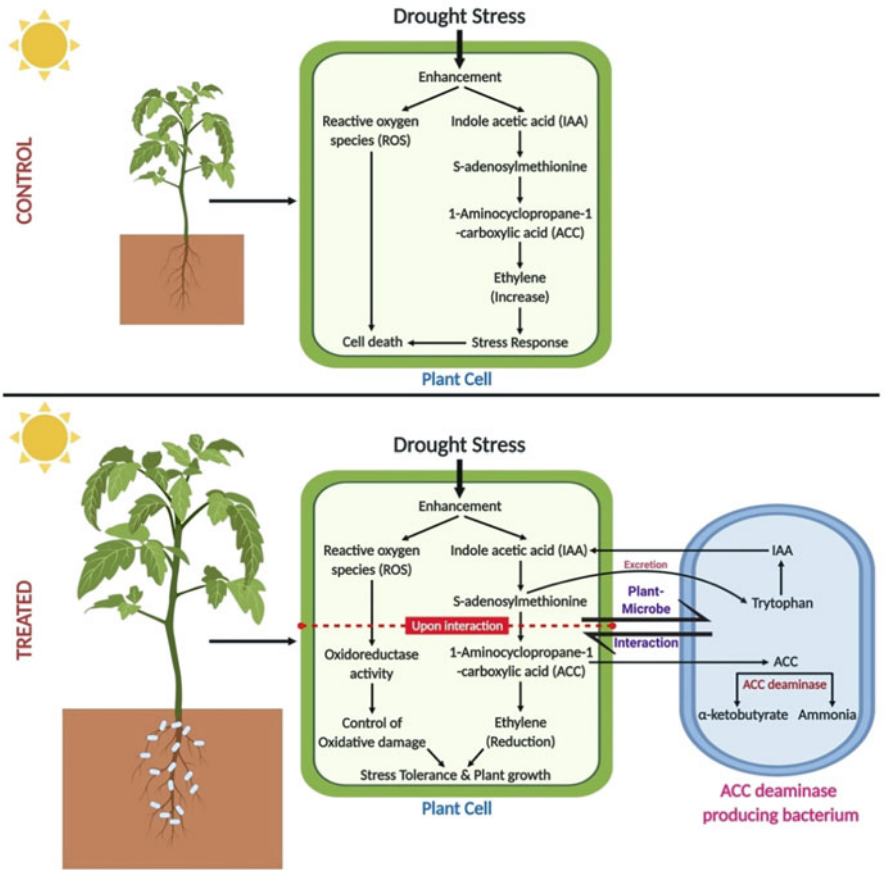

Fig. 1.3 Mechanism of action of ACC deaminase-producing PGPR for the induction of drought stress tolerance in plants (source: adopted from Gowtham et al. 2020)

grown in iron-limiting conditions, Terano et al. (2002) observed a new protein band of 75 kDa on the cell wall of *P. fluorescens* and increased development of protein of 54 kDa. This protein's expression may be involved in the siderophore-mediated iron-uptake process.

Siderophore is classified into three groups based on the iron-coordinating functional group. Hydroxamates (mycobactin and exochelin), catechols (enterobactin and vibriobactin), and thiazolines are examples of these compounds (pyochelin and yersiniabactin) (Essen et al. 2007). Iron solubilization, transport, and storage are the primary functions of siderophores (Stephan et al. 1993). There is a lot of evidence that various plant species can absorb bacterial Fe^{3+} siderophore complexes, and this process is important for plant iron absorption, particularly in calcareous soils (Masalha et al. 2000). A decrease often followed increased plant growth caused by *Pseudomonas* strains in root pathogen populations. There is strong evidence that

siderophore-mediated iron competition plays a direct role in these PGPR strains' biocontrol function (Loper and Buyer 1991).

For many plant diseases, the feasibility of using induced systemic resistance to protect plants has been demonstrated. Plants inoculated with the PGPR *P. putida* and *S. marcescens* biocontrols, for example, were covered against the cucumber pathogen *P. syringae* pv. *lachrymans* (Bashan and de-Bashan 2005). The role of siderophore concentration developed by *Pseudomonas* sp. in suppressing tomato bacterial wilt was investigated by Jagadeesh et al. (2001). Certain fluorescent *Pseudomonas* sp. strains synthesize siderophores that suppress soilborne plant diseases by opposing pathogen growth by sequestering iron from the atmosphere (Bashan and de-Bashan 2005). The pathogenic fungus *F. oxysporum* in tomato can be regulated more effectively by a mutant strain of *P. putida* that overproduces siderophores than the wild bacterium. The pyoverdine siderophore function produced by many *Pseudomonas* sp. in the control of *Pythium* and *Fusarium* species has been demonstrated in the rhizosphere microbial community structure (Yang and Crowley 2000). The role of iron and catechol siderophore concentrations in inducing systemic resistance in cucumber against *Colletotrichum orbiculare* infection was investigated by Press et al. (2001).

1.4 Secondary Metabolite Production

The research of rhizobacteria isolated from the rhizospheres of important medicinal plants is extremely important because they are well known for promoting plant growth and producing important metabolites (Solaiman and Anawar 2015). The inhibition or destruction of one organism by a metabolite created by another organism is known as antibiosis. Broad-spectrum antibiotics are agonists that develop strong growth inhibitory compounds effective against a wide range of microorganisms. Antibiotic production has been identified as a powerful mode of disease suppression in which the pathogen's development and/or activity is thought to be directly inhibited (Handelsman and Stabb 1996). Tomashow and Weller (1988) made the first convincing experiment on the bacterium-produced antibiotics that restrains plant disease in an ecosystem. The direct and indirect isolation techniques are used to isolate a wide variety of antifungal rhizobacteria from maize, barley, and chicory, including *P. fluorescens*, *P. cepacia*, *Serratia liquefaciens*, *S. plymuthica*, *Erwinia herbicola*, and *Bacillus* sp. (Lambert et al. 1987).

Many bacteria developed antimicrobial compounds in significant amounts (Solaiman and Anawar 2015). Pseudomonads inhibited soilborne fungal pathogens by producing antifungal compounds according to Dwivedi and Johri (2003). Using bioautography, the antifungal activity of *Pseudomonas cepacia* B37w was linked to the development of pyrrolnitrin, a particular antifungal compound (Burkhead et al. 1994). A novel antifungal compound, maltophilin, was developed by *Stenotrophomonas maltophilia* R3089 strain that was isolated from rape plants' rhizosphere (Jakobi et al. 1996). Compared to their wild type, nonmotile Tn5 transposon mutants of *Fusarium oxysporum* f.sp. *radicis-lycopersici* antagonistic

biocontrol strain *Pseudomonas chlororaphis* produce phenazine-1-carboxamide as the active metabolite which is at least 1000 times less successful in competitive tomato root-tip colonization (Chin-A-Woeng et al. 1998). From a sugar beet rhizobacterium, *Stenotrophomonas* sp. strain SB-K88, Nakayama et al. (1999) isolated three antifungal compounds known as xanthobaccins A, B, and C. They hypothesized that xanthobaccins produced by the bacterium played a crucial role in inhibiting damping-off disease in sugar beet. A fluorescent *Pseudomonas* sp. isolated from maize rhizosphere was found to be strongly antagonistic to maize foot, collar, and root rots along with wilting diseases caused by different species of *Fusarium* by producing different plant growth-promoting metabolites and fungal antibiotics (Pal et al. 2001). The three main antifungal compounds were found to be isomers of iturin A, a cyclic lipopeptide antibiotic produced by *Bacillus amyloliquefaciens* and used as a biocontrol agent against *Rhizoctonia solani* and other fungal plant pathogens, according to fast atom bombardment mass spectrometry/mass spectrometry collision-induced dissociation study (Yu et al. 2002).

Based on NMR and MS results, the antifungal metabolite produced by *Pseudomonas aeruginosa* PUPa3 has been classified as phenazine-1-carboxamide, which has broad-spectrum antifungal activity against a variety of phytopathogenic fungi (Kumar et al. 2005). Bacteria isolated from canola and soybean plants produced the antifungal organic volatile compounds (benzothiazole, cyclohexanol, n-decanal, etc.) that may play a key role in inhibiting sclerotial activity, limiting ascospore development, and lowering disease levels caused by *Sclerotinia sclerotiorum* (Fernando et al. 2005). *Pseudomonas fluorescens* produces antifungal metabolites such as pyrrolnitrin and pyoluteorin including 2,4-diacetylphloroglucinol and the evidence from the research suggests that these compounds are held in a balance that can be affected by certain plant and microbial phenolics (Baehler et al. 2005). A new nitrogen-containing heterocyclic antibiotic compound, "amino (5-(4-methoxyphenyl)-2-methyl-2-(thiophen-2-yl)-2,3-dihydrofuran-3-yl)methanol" (AMTM), was produced by *Delftia tsuruhatensis* WGR–UOM–BT1, a novel rhizobacterium from *Rauwolfia serpentina* with multiple PGPR properties for suppressing fungal phytopathogens (Prasannakumar et al. 2015).

1.4.1 Production of Hydrolytic Enzymes

Hydrolytic enzymes such as chitinases, β-1,3-glucanases, proteases, and lipases are among these substances. Any of these hydrolytic enzymes can be synthesized by a variety of *Pseudomonas* and *Bacillus* species. Extracellular chitinase and β-1,3-glucanase are produced by *Pseudomonas stutzeri*, which lyses the pathogen *Fusarium* sp. (Bashan and de-Bashan 2005). Fusaric acid (produced by *Fusarium*) can be hydrolyzed by *B. cepacia* and *Cladosporium werneckii*, causing severe plant damage.

Chitinases are glycol hydrolases that catalyze the hydrolytic degradation of chitin and non-soluble linear β-1,4-linked polymer of N-acetylglucosamine (GlcNAc) (Kurita 2001). Since these pathogenic fungi have a major cell wall component of

chitin, chitinase provided by chitinolytic rhizobacteria can degrade; rhizobacterial isolates' chitinolytic capacity had the potential to reduce soilborne root disease of many crop plants. Isolating possible chitinolytic rhizobacteria is thus a crucial step in the development of biopesticides. Three isolates of *Micromonospora carbonacea*, *Serratia marcescens*, and *Streptomyces viridodiasticus* produced high levels of chitinase that suppressed the growth of *Sclerotinia minor* (El-Tarabily et al. 2000). Aktuganov et al. (2003) investigated 70 *Bacillus* sp. strains that were antagonistic to phytopathogenic fungi and discovered that 19 of them had chitinolytic activity. Kamil et al. (2007) isolated 400 bacteria from the rhizospheres of maize, wheat, and rice plants and identified potent chitinolytic rhizobacteria in a minimal salt medium containing colloidal chitin as the sole carbon and energy source. In vitro, strains MS1 and MS3 inhibited the growth of all pathogenic fungi that were studied. Ajit et al. (2006) isolated fluorescent pseudomonads antagonistic to *F. oxysporum* f. sp. *dianthi*, the pathogen that causes carnation vascular wilt, and linked disease defense chitinase activity. Mycelial growth was also substantially inhibited by cell-free bacterial culture filtrate from chitin-containing media. According to Western blot analysis, chitinase is found in two isoforms with molecular masses of 43 kDa and 18.5 kDa.

Bacillus cereus CRS7-purified chitinase had a molecular weight of 47 kDa (Kishore and Pande 2007). Extracellular chitinase formed by the super-producing mutant strain *Serratia marcescens* M-1 was studied by Duzhak et al. (2009). They looked at four extracellular proteins with chitinase activity capable of binding chitin substrates, weighing 62, 54, 52, and 21 kDa. The proteins ChiA, ChiB, ChiC, and CBP21 were described as typical *S. marcescens* chitinases based on the data obtained. Furthermore, Kishore and Pande (2007) used chitinolytic *B. cereus* CRS7 and non-chitinolytic *Pseudomonas fluorescens* CRS31 to combat Botrytis gray mold, demonstrating the role of chitinase in plant disease management. Glucanases are another essential group of hydrolytic enzymes that degrade the phytopathogenic fungal cell wall. The rhizosphere proliferation of various phyto-pathogenic fungi was inhibited by β-1,3-glucanase-producing strain of *Pseudomonas cepacia* (Fridlender et al. 1993). The combined activity of the two hydrolytic enzymes chitinase and β-1,3-glucanase was more efficient than either enzyme alone in inhibiting fungal pathogens (Tanaka and Watanabe 1995). Inoculation of rice roots with endoglucanase-producing diazotrophs can boost root colonization and stimulate root and plant development. The ability to colonize plant roots will increase the plant's biological nitrogen-fixing activity (Asilah et al. 2009).

1.5 Future Prospective and Conclusion

The availability of effective biocontrol agent formulations including survival during storage, rapid proliferation, and colonization ability after application plays a vital role in the success of biological control of plant diseases. One of the mechanisms for promoting growth by PGPR may be the activation of the host defense system and it warrants further study. While many biocontrol agents can control plant pathogens,

only a few commercial formulations have demonstrated consistently strong and stable efficacy in the field. The conflicting output of biocontrol agents under field study may be due to their ecological competence, soil, and microbiological factors. On the other hand, several studies showed that the field techniques performed consistently over time. Finally, safe biocontrol agent formulations are critical for subsistence gladiolus farming, where soilborne diseases are the key crisis and fungicide treatments are prohibitively expensive. When commercialized, the talc-based strain mixture formulation can become a favored input in integrated disease management systems. Further research on cost-effectiveness, performance evaluation using several pathogens, and/or evaluation in other agroclimatic regions will be needed to explore the formulation's commercialization.

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