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PLANT GROWTH PROMOTING RHIZOBACTERIA: A REVIEW ARTICLE

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ABSTRACT

Sustainable agriculture is vitally important in today's world because it offers the potential to meet our future agricultural needs, something that conventional agriculture will not be able to do. Soil microorganisms with beneficial activity on plant growth and health represent an attractive alternative to conventional agricultural practice. Plant Growth-Promoting Rhizobacteria (PGPR) are naturally occurring soil bacteria that aggressively colonize plant roots and benefit plants by providing growth promotion. PGPR are associated with plant roots and augment plant productivity and immunity; however, recent work by several groups shows that PGPR also elicit so-called 'induced systemic tolerance' to salt and drought. PGPR might also increase nutrient uptake from soils, thus reducing the need for fertilizers and preventing the accumulation of nitrates and phosphates in agricultural soils. Scientific researches involve multidisciplinary approaches to understand adaptation of PGPR, effects on plant physiology and growth, induced systemic resistance, biocontrol of plant pathogens, bio fertilization, and potential green alternative for plant productivity, viability of co inoculating, plant microorganism interactions, and mechanisms of root colonization.

INTRODUCTION

The soil attached to the root system is a hot spot of microbial abundance and the activity is due to the presence of root exudates and rhizodeposits (Smalla *et al.,* 2006). Plant root exudates attract microbes and feed them and, in turn, the plants often benefits from the microbes. Soil microorganisms play a vital role in soil processes which have direct bearing on productivity of crop plants. Effective functioning of introduced bioinoculants is possible only by exploring the large pool of indigenous soil microbes (Hill *et al.,* 2000). Many microorganisms are attracted by nutrients exuded from plant roots and this "rhizosphere effect" was first described by Hiltner (Hiltner, 1904). The rhizosphere and rhizoplane are colonized more intensively by microorganisms than the other regions of the soil. Some of these microorganisms not only benefited from the nutrients secreted by the plant roots but also beneficially influence the plants, resulting in a stimulation of their growth. For instance, rhizobacteria can fix atmospheric nitrogen, which is subsequently used by the plants, thereby improving plant growth in the soil deficient of nitrogen. Other rhizobacteria can directly promote the plant growth by the production of hormones. These rhizobacteria positively influence plant growth and health and often referred as Plant Growth Promoting Rhizobacteria (PGPR).

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Direct use of microorganisms to promote plant growth and to control plant pests continues to be an area of rapidly expanding research. Rhizosphere colonization is one of the first steps in the pathogenesis of soil borne microorganisms. It is also crucial for the microbial inoculants to be used as biofertilizers, biocontrol agents, phytostimulators, and bioremediators. *Pseudomonas* spp. is often used as model root-colonizing bacteria (Lugtenberg *et al*., 2001). Motile rhizobacteria may colonize the rhizosphere more profusely than the non-motile organisms resulting in better rhizosphere activity and nutrient transformation. They also eliminate deleterious rhizobacteria from the rhizosphere by niche exclusion thereby better plant growth (Weller, 1988). The present review is an effort to elucidate the concept of rhizobacteria in the current scenario and their Underlying mechanisms of plant growth promotion with recent updates. The latest paradigms of a wide range of applications of these beneficial rhizobacteria in different agro-ecosystems have been presented explicitly to garner broad perspectives regarding their functioning and applicability.

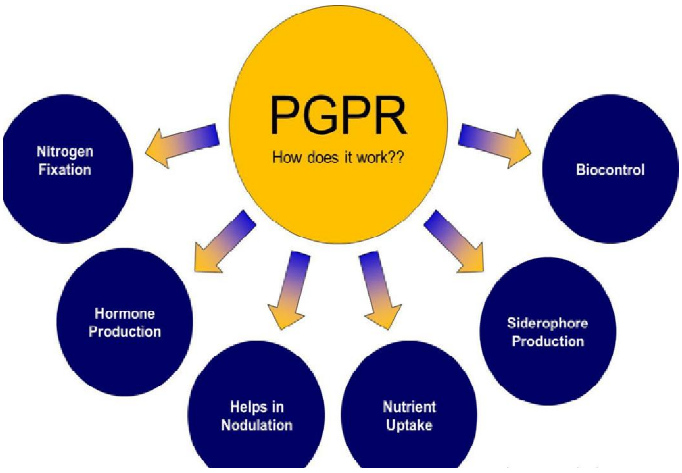
Rhizosphere

The root system, which was traditionally thought to provide anchorage and uptake of nutrients and water, is in fact a chemical factory that mediates numerous underground interactions (Badri *et al.,* 2009). The narrow zone of soil directly surrounding the root system is referred to as rhizosphere (Walker *et al.,* 2003), while the term 'rhizobacteria' implies a group of rhizosphere bacteria competent in colonizing the root environment (Kloepper *et al.,* 1991). Plant roots also synthesize, accumulate, and secrete a diverse array of compounds (Walker *et al.,* 2003). These compounds secreted by plant roots act as chemical attractants for a vast number of heterogeneous, diverse and actively metabolizing soil microbial communities. The composition of these exudates is dependent upon the physiological status and species of plants and microorganisms (Kang *et al.,* 2010). These exudates also promote the plant-beneficial symbiotic interactions and inhibit the growth of the competing plant species (Nardi *et al.,* 2000). Largely, three separate but interacting components are recognized in the rhizosphere: the rhizosphere (soil), the rhizoplane, and the root itself. Of these, the rhizosphere is the zone of soil influenced by roots through the release of substrates that affect microbial activity. The rhizoplane, on the other hand, is the root surface including the strongly adhering soil particles while the root itself is a component of the system, because many micro-organisms (like endophytes) also colonize the root tissues (Barea *et al.,* 2005).

Plant growth promoting Rhizobacteria

Different bacterial genera are vital components of soils. They are involved in various biotic activities of the soil ecosystem to make it dynamic for nutrient turn over and sustainable for crop production (Ahemad *et al.,* 2009; Chandler *et al.,* 2008). The bacteria lodging around/in the plant roots (rhizobacteria) are more versatile in transforming, mobilizing, solubilising the nutrients compared to those from bulk soils (Hayat *et al.,* 2010). Therefore, the rhizobacteria are the dominant deriving forces in recycling the soil nutrients and consequently, they are crucial for soil fertility (Glick, 2012). The plant growth promoting rhizobacteria (PGPR), are characterized by the following inherent distinctiveness's:

(i) They must be proficient to colonize the root surface.
(ii) They must survive, multiply and compete with other microbiota; at least for the time needed to express their plant growth promotion/protection activities.
(iii) They must promote plant growth (Kloepper, 1994).



Some common examples of PGPR genera exhibiting plant growth promoting activity are: *Pseudomonas, Azospirillum, Azotobacter, Bacillus, Burkholdaria, Enterobacter, Rhizobium, Erwinia, Mycobacterium, Mesorhizobium, Flavobacterium,* etc.

Mechanisms of plant growth promotion

PGPR are beneficial for plant growth and also referred as Yield Increasing Bacteria (YIB). They can affect plant growth and yield in a number of ways and enhancement of vegetative and reproductive growth is documented in a range of crops like cereals, pulses, ornamentals, vegetables, plantation crops and some trees. Treatments with PGPR increase germination percentage, seedling vigour, emergence, plant stand, root and shoot growth, total biomass of the plants, seed weight, early flowering, grains, fodder and fruit yields etc., (van Loon *et al*., 1998; Ramamoorthy *et al*., 2001). Several mechanisms (Fig 1) have been postulated to explain how Plant Growth-Promoting Rhizobacteria (PGPR) stimulates plant growth. These mechanisms are broadly categorized as Direct or indirect (Glick, 1995). PGPR directly contribute to the plant growth are phytohormone production like auxins, cytokinins and gibberellins, enhancing plant nutrition by solubilization of minerals like phosphorus and iron, production of siderophores and enzymes, lowering of ethylene levels and induction of systemic resistance (Bhattacharyya and Jha, 2012). PGPR indirectly benefit the plant growth by the biocontrol of deleterious microorganisms or root pathogens that inhibit plant growth, including antibiotic production, parasitism, competition for nutrients and niches within the rhizosphere, synthesis of extracellular enzymes to hydrolyze the fungal cell wall, decreasing pollutant toxicity (Bhattacharyya and Jha, 2012; Podile and Kishore , 2006; Zahir *et al.,* 2003).

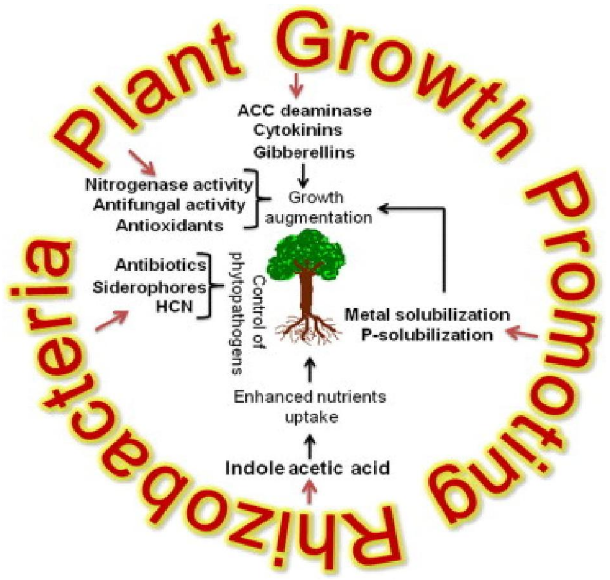


Fig. 1. Mechanism of plant growth promotion by rhizobacteria

Direct mechanisms

Nitrogen fixation

Nitrogen (N) is the most vital nutrient for plant growth and productivity. Although, there is about 78% N_2 in the atmosphere, it is unavailable to the growing plants. The atmospheric N_2 is converted into plant-utilizable forms by Biological N_2 fixation (BNF) which changes nitrogen to ammonia by nitrogen fixing microorganisms using a complex enzyme system known as nitrogenase (Kim and Rees, 1994). Biological nitrogen fixation occurs, generally at mild temperatures, by nitrogen fixing microorganisms, which are widely distributed in nature (Raymond *et al.,* 2004). Zhang *et al.,* 1996 recognized the species of PGPR bacteria, which increased the growth of Legumes plant, root development and nitrogen fixation especially in the temperature lower than the optimized condition of the Rzts-Root Zone temperature. 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 Mg ATP 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).

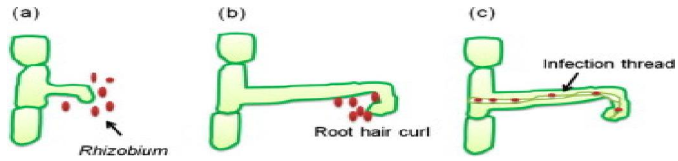


Figure 2

The nodulation process (a) Interaction of rhizobial rhicadhesin with host lectins and rhizobial attachment with root cells. (b) Excretion of nod factors by rhizobia causes root hair curling. (c) Rhizobia penetrate root hair and form an infection thread through which they penetrate the cortical cells and form bacteroid state thereby nodules are formed.Nitrogen fixing organisms are generally categorized as (a) symbiotic N_2 fixing bacteria including members of the family rhizobiaceae which forms symbiosis with leguminous plants (e.g. rhizobia) (Ahemad and Khan, 2012d and Zahran, 2001) and non-leguminous trees (e.g. Frankia) and (b) non-symbiotic (free living, associative and endophytes) nitrogen fixing forms such as cyanobacteria (Anabaena**,** Nostoc), Azospirillum**,** Azotobacter**,** Gluconoacetobacter diazotrophicus and Azocarus etc. (Bhattacharyya and Jha, 2012). However, non-symbiotic nitrogen fixing bacteria provide only a small amount of the fixed nitrogen that the bacterially-associated host plant requires (Glick, 2012). Symbiotic nitrogen fixing rhizobia within the rhizobiaceae family (α-proteobacteria) infect and establish symbiotic relationship with the roots of leguminous plants. The establishment of the symbiosis involves a complex interplay between host and symbiont (Giordano and Hirsch, 2004) resulting in the formation of the nodules wherein the rhizobia colonize as intracellular symbionts (Fig. 2).

Phosphate Solubilization

Since P is an essential macronutrient for plant growth and has only limited bioavailability, it is considered to be one of the elements that limit plant growth (Feng *et al*., 2004). 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, phosphodiesters, and phosphotriesters (Khan *et al*., 2007). Solubilisation and mineralization of P by Phosphate-Solubilizing Bacteria (PSB) is one of the most important bacterial physiological traits in soil biogeochemical cycles (Fig.3). (Jeffries *et al.,* 2003), as well as in plant growth Promotion by PGPB (Rodriguez and Fraga 1999; Richardson 2001). Bacterial genera like Azotobacter, Bacillus, Beijerinckia, Burkholderia, Enterobacter, Erwinia**,** Flavobacterium**,** Microbacterium**,** Pseudomonas, Rhizobium and Serratia are reported as the most significant phosphate solubilizing bacteria (Bhattacharyya and Jha, 2012). Typically, the solubilization of inorganic phosphorus occurs as a consequence of the action of low molecular weight organic acids which are synthesized by various soil bacteria (Zaidi *et al.,* 2009). Conversely, the mineralization of organic phosphorus occurs through the synthesis of a variety of different phosphatases, catalyzing the hydrolysis of phosphoric esters (Glick, 2012). Importantly, phosphate solubilization and mineralization can coexist in the same bacterial strain (Tao *et al.,* 2008). Besides providing P to the plants, the PS bacteria also augment the growth of plants by stimulating the efficiency of BNF, enhancing the availability of other trace elements (such as iron, zinc) and by synthesizing important plant growth promoting substances (Ponmurugan and Gopi, 2006**;** Mittal *et al*., 2008). To make this form of P available for plant nutrition, it must be hydrolyzed to inorganic P by means of acid and alkaline phosphatase enzymes. Because the pH of most soils ranges from acidic to neutral values acid phosphatases should play the major role in this process (Rodríguez and Fraga, 1999). The possibility of enhancing P uptake of crops by artificial inoculation with P-solubilising strains of rhizobacteria presents an immense interest to agricultural microbiologists.

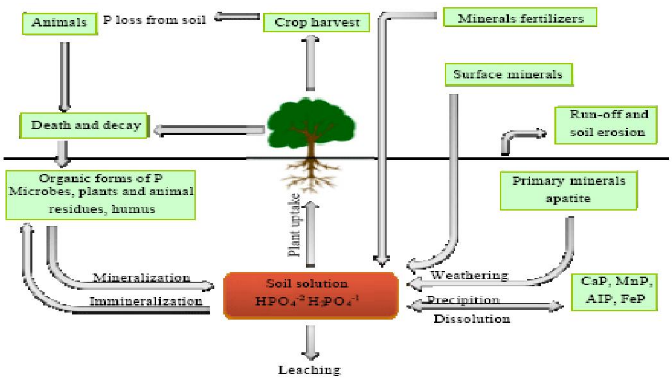


Fig. 3. Solubilization and mineralization of P

Sequestering of iron by production of siderophores

Iron-chelating molecules termed siderophores are generally less than 1000 molecular weight and are produced by many microorganisms. Iron is an essential micronutrient for plants as it serves as a cofactor of many enzymes with redox activity and it is required in a number of major physiological processes like N_2fixation, photosynthesis, respiration, etc. To meet their iron requirement, microorganisms and plants have evolved specific mechanisms to chelate insoluble iron through the release of siderophores and uptake of iron-siderophore complexes through specific outer membrane receptor proteins (Sharma and Johri, 2003). These siderophores can be of different types: hydroxamates, phenol-catecholates, and carboxylates (Podile and Kishore, 2006). The synthesis of siderophores in bacteria is induced by the low level of Fe3+ and in acid soil, where solubility and availability grow, their protective effect comes down. Microbial siderophores in the rhizosphere are frequently associated with biocontrol activities and not with plant nutrition (Vessey, 2003). (Fig 4-5). In a report, Glick *et al.,* 1995 measured the 11 pseudomonas strains ability in increasing the canola root length under the gnotobiotic conditions.

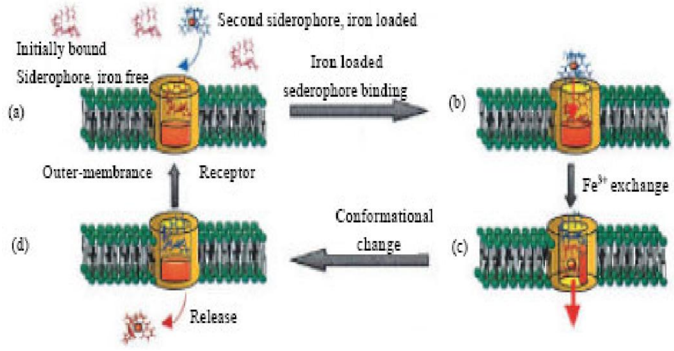


Fig. 4. The siderophores shuttle iron delivery mechanism. Adopted from Stintizi *et al*. (2002)

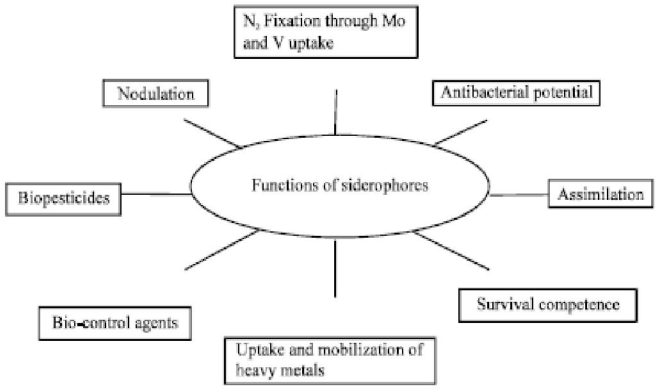


Fig. 5. Impact of microbially secreted siderophores on plant growth

Synthesis of Plant Hormones

Phytohormones are signal molecules acting as chemical messengers and play a fundamental role as growth and development regulators in the plants. Phytohormones are organic compounds that in extremely low concentrations influence biochemical, physiological and morphological processes in plants, and their synthesis is finely regulated (Fuentes-Ramírez and Caballero-Mellado, 2006). With the production of different phytohormones like indole-3-acetic acid (IAA), gibberellic acid and cytokinins PGPR can increase root surface and length and promote in this way plant development (Kloepper *et al*., 2007). IAA (auxin) is the most quantitatively important phytohormone produced by PGPR, and treatment with auxin-producing rhizobacteria increased the plant growth (Vessey, 2003). Production of other phytohormones by biofertilizing-PGPR has been identified, but not nearly to the same extent as bacteria which produce IAA (Vessey, 2003). A few PGPR strains were reported to produce cytokinins and gibberellins (gibberellic acid) (Gutiérrez-Mañero *et al*., 2001, Vessey, 2003). Bacteria like Azospirillum and Pseudomonas spp. produce cytokinins and gibberellins, in addition to IAA (Gaudin *et al.,* 1994). Studies of Glick (1998) showed that many PGPR have the capability to produce 1-aminocyclopropane-1-carboxylate (ACC) deaminase, an enzyme which cleaves ACC, the immediate precursor of ethylene in the biosynthetic pathway for ethylene in plants (Glick *et al.,* 1998).

In Direct mechanisms

Biocontrol

The application of microorganisms to control diseases, which is a form of biological control, is an environment-friendly approach. In general, competition for nutrients, niche exclusion, induced systemic resistance and antifungal metabolites production are the chief modes of biocontrol activity in PGPR (Lugtenberg and Kamilova, 2009). The major indirect mechanism of plant growth promotion in rhizobacteria is through acting as biocontrol agents (Glick, 2012). Many rhizobacteria have been reported to produce antifungal metabolites like, HCN, phenazines, pyrrolnitrin, 2, 4-diacetylphloroglucinol, pyoluteorin, viscosinamide and tensin (Bhattacharyya and Jha, 2012). Interaction of some rhizobacteria with the plant roots can result in plant resistance against some pathogenic bacteria, fungi, and viruses. This phenomenon is called induced systemic resistance (ISR) (Lugtenberg and Kamilova, 2009).

Moreover, ISR involves jasmonate and ethylene signaling within the plant and these hormones stimulate the host plant's defense responses against a variety of plant pathogens (Glick, 2012). *A.brasilense* cells contain a low molecular-weight compound that inhibits germination and growth of the radicle of Egyptian broom rape seeds (*Orobanche aegyptiaca),* a specific weed parasite of sunflower (Dadon *et al.,* 2004). Azospirillum spp. inhibited germination of the parasitic striga weed (witchweed) seeds (*Striga hermonthica*) that infest fields of tropical sorghum, thereby promoting growth of sorghum (Bouillant *et al.,* 1997). Based on their mechanism of action, PGPR can be categorized into three general forms (Table 1) such as biofertilizer (a substance that contains live microorganisms with biological nitrogen fixation and phosphorus solubilisation capabilities), Phytostimulator (microorganism with the ability to produce phytohormones) and biopesticide (microorganisms that promote plant growth by controlling phytopathogenic agents) (Bhattacharyya and Jha, 2012).

Mitigation of abiotic stresses by PGPR

Soil salinity in arid regions is frequently an important limiting factor for cultivating agricultural crops. Although many technologies have been implicated in the improvement of salt tolerance, only PGPR-elicited plant tolerance against salt stress has been previously studied (Mayak *et al.,* 2004). IST to salt stress was also noted in a new study with Arabidopsis using *Bacillus subtilis* GB03, a species that has previously been used as a commercial biological control agent (Zhang *et al.,* 2008). Term 'induced systemic tolerance' (IST) for PGPR-induced physical and chemical changes in plants that result in enhanced tolerance to abiotic stress. IST elicited by PGPR against drought, salt and fertility stresses underground (root) and aboveground (shoot). Broken arrows indicate bioactive compounds secreted by PGPR; solid arrows indicate plant compounds affected by bacterial components. Some PGPR strains, indicated in red on the plant roots, produce cytokinins and antioxidants such as catalase, which result in ABA accumulation and ROS degradation, respectively and Degradation of the ethylene precursor ACC by bacterial ACC deaminase releases plant stress and rescues normal plant

Table 1. Terms adopted for classified mechanisms by which plant growth promoting bacteria stimulate plant growth

Term	Definition	Mechanism	Reference
Bio fertilizer	A substance which contains live microorganisms which, when applied on the seed, plant surface or the soil, colonizes the Rhizosphere or the interior of the plant and promotes growth through increased supply or availability of primary nutrients for the host plant	-Biological nitrogen fixation. -Utilization of insoluble forms of phosphorus	Vessey, 2003; Somers *et al.,* 2004; Fuentes-Ramírez and Caballero-Mellado, 2006.
Phytostimulator	Microorganism with the ability to produce or change the concentration of growth regulators such as indole - acetic acid, gibberellic acid, cytokinins and ethylene	-Production of phytohormones (auxins, cytokinins and gibberellins) -Decreased ethylene concentration (in the interior of the plant)	Lugtenberg *et al.,* 2002; Somers *et al.,* 2004.
Biopesticide or biocontrol agent	Microorganisms that promote plant growth through the control of phytopathogenic agents, mainly for the production of antibiotics and antifungal metabolites.	-production of antibiotics (siderophores, HCN, antifungal metabolites). -Production of enzymes that degrade the cellular wall of the fungi. -Competitive exclusion. -Acquired and Induced systemic resistance.	Vessey, 2003; Somers *et al.,* 2004; Chandler *et al.,* 2008.

(Source- Viveros *et al.,* 2010)

growth under drought and salt stresses and. The volatiles emitted by PGPR down regulate hkt1 expression in roots but up regulate it in shoot tissues, orchestrating lower Na^+ levels and recirculation of Na^+ in the whole plant under high salt conditions. Production by PGPR of IAA or unknown determinants can increase root length, root surface area and the number of root tips, leading to enhanced uptake of nitrate and phosphorous (Fig 6). Under high NaCl concentration, inoculation of wheat with *A. lipoferum* reduced some of the deleterious effects of NaCl (Bacilio *et al.,* 2004). Inoculation with *Azospirillium* alleviated the stress on wheat plants grown under drought conditions (El-Komy *et al.,* 2003).

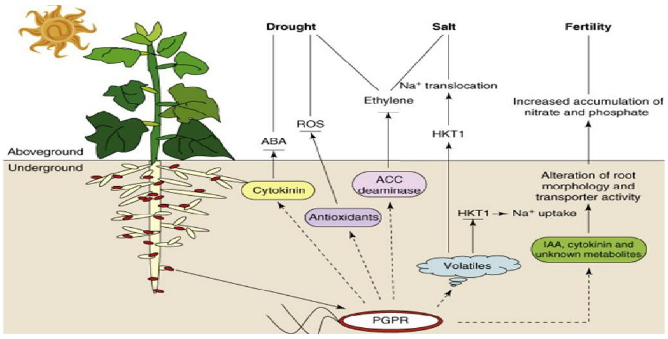


Fig. 6 PGPR against drought, salt and fertility stresses.

Use of PGPR on commercial scale

In the mid1990s in the USA, *B. subtilis* started to be used as seed dressing, with registrations in more than seven crops and application to more than 2 million ha (Backmann *et al.,* 1994). This was the first major commercial success in the use of an antagonist. Commercial development has already been accomplished with two products marketed as Kodiak and Epic (Gustafson inc.), in which two different *Bacillus subtilis* biocontrol strains were combined with a fungicide (Carboxin-PCNB-metalaxyl) for use against soil borne diseases. The application of five commercial chitosan-based formulations of carefully chosen PGPR developed at Auburn University, USA has previously shown demonstrable increase in the growth of nursery-raised plants such as cucumber, pepper and tomato among others. Seedlings of three *indica* rice cultivars, IR24, IP50 and Jyothi raised in rice field soil amended with each of the formulations in a 1:40 (formulation: soil) ratio have shown significant two-fold increase in root and shoot length, and grain yield. The observations do suggest that application of such commercial bacterial formulations can serve as microbial inoculants for the improvement of rice growth (Vasudevan *et al.,* 2002). PGPR are effective as a bio enhancer and biofertilizer for banana cultivation. The inoculation also increased the N yield and fixed N_2 in association with banana roots subsequently increased the yield, improved the physical attributes of fruit quality and initiated early flowering. (Baset *et al*., 2010). Inoculation of oilseed (*Salicornia bigelovii Torr.*) with PGPR has been reported to increase plant biomass, palmitic acid, total N and protein content. The PGPR inoculation also increased P content through P solubilization (Bashan *et al.,* 2000). The effects of plant growth promoting rhizobacteria (PGPR) on the rooting and root growth of semi-hardwood and hardwood kiwifruit stem cuttings were investigated by Erturk *et al*., 2010.

The PGPR used were *Bacillus RC23, Paenibacillus polymyxa RC05, Bacillus subtilis OSU142, Bacillus RC03, Comamonas acidovorans RC41, Bacillus megaterium RC01* and *Bacillus simplex RC19.* All the bacteria showed indole-3-acetic acid (IAA) producing capacity. Of the various rhizospheric bacteria, Pseudomonas sp. are aggressive colonizers of the rhizosphere of various crop plants (Schroth and Hancock, 1982) and have a broad spectrum of antagonistic activity against plant pathogens (Davison1988). The antibiotic produced by *Pseudomonas fluorescens* was found to control damping-off of cotton seedlings caused by R. solani (Howell 1979). Among *Pseudomonas* species, *Pseudomonas aeruginosa,* a plant growth promoting rhizobacterium has been found to be an effective biocontrol agent of root pathogens (Izhar 1995, Burdman *et al.,* 1996) *Septoria tritici (Mycosphaerella graminicola*) was suppressed by *P. aeruginosa* strain leci. Schonbick *et al.,* 1980 isolated a *B. subtilis* strain whose metabolites are able to induce systemic resistance against powdery mildew on Barley. Combined inoculation of *A. brasilense* and the phosphate-solubilizing bacteria *Pseudomonas strica* or *Bacillus polymyxa* on field grown sorghum significantly increased grain and dry matter yields and N and P uptake as compared with single inoculation of individual organisms (Alagawadi & Gaur, 1992).

Integration and mixtures of PGPR

In nature biocontrol results from mixtures of antagonists, rather from high populations of a single antagonist**.** Consequently, application of a mixture of introduced biocontrol agents would more closely mimic the natural situation and may broaden the spectrum, enhance the efficacy and reliability of biocontrol (Duffy and Weller, 1995). Combination of various mechanisms of biocontrol is useful in achieving the goal without genetic engineering (Janisiewicz, 1996). PGPR strains INR 7 (*Bacillus pumilus*). GBO3 (*Bacillus subtilis)*, and ME1 *(Curtobacterium flccumfaciens)* were tested alone and in combinations for biocontrol against *Colletotrichum orbiculare* (causing anthracnose), *Pseudomonas syringae pv. Lachrymans* (causing angular leaf spot), and *Erwinia tracheiphila* (causing cucurbit wilt disease) (Raupach and Kloepper, 1998). Studies on combinations of biocontrol agents for plant disease control have included mixtures of fungi (Budge *et al*., 1995; Datnoff *et al.,* 1993, 1995; De Boer *et al.,* 1997; Paulitz *et al.,* 1990), mixtures of fungi and bacteria (Duffy *et al.,* 1996; Duffy and Weller, 1995; Hassan *et al.,* 1997). Combinations of a strain of *Trichoderma koningii* with different Pseudomonas spp. isolates provided greater suppression of take-all disease than either the fungus or the bacterium alone (Duffy *et al.,* 1996). Similarly, chitinase-producing *Streptomyces spp*. and *Bacillus cereus* isolates used in conjunction with antibiotic-producing *P. fluorescens and Burkholderia cepacia* isolates had a synergistic effect on the suppression of rice sheath blight (Sung and Chung, 1997). Positive and negative interactions of introduced microorganisms and indigenous microflora can influence their performance in the rhizosphere. For example, two groups of microorganisms that occupy the same ecological niche and have the same nutritional requirements are bound to compete for nutrients (Bakker *et al.,* 1988; Fukui *et al.,* 1994; Janisiewicz and Bors, 1995). Siderophore-mediated competition for iron between the two biocontrol agents *P. putida* WCS358 and *P. fluorescens* WCS374 decreased colonization of radish roots by the latter strain (Raaijmakers *et al.,* 1995).

Challenges in Field Application of PGPR

The application of PGPR for control of fungal pathogens in greenhouse systems shows considerable promise (Paulitz and Belanger 2001) due in part to the consistent environmental conditions and high incidence of fungal disease in greenhouses. Achieving consistent performance in the field where there is heterogeneity of abiotic and biotic factors and competition with indigenous organisms is more difficult. Knowledge of these factors can aid in determination of optimal concentration, timing and placement of inoculants, and of soil and crop management strategies to enhance survival and proliferation of the inoculants (Bowen and 1999; Gardener and Fravel 2002). The concept of engineering or managing the rhizosphere to enhance PGPR function by manipulation of the host plant, substrates for PGPR, or through agronomic practices, is gaining increasing attention (Mansouri *et al.,* 2002). Development of better formulations to ensure survival and activity in the field and compatibility with chemical and biological seed treatments is another area of focus; approaches include optimization of growth conditions prior to formulation and development of improved carriers and application technology (Date, R. A. 2001; Yardin *et al*., 2000).

Conclusions

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. Identification of different mechanisms involved in plant-rhizosphere microorganism interaction opened new possibilities to design strategies for improving crop yields. Along this, biotechnology can be applied to further improve strains that have PGPR qualities in order to create transgenic strains that combine multiple mechanisms of action. Our understanding of plant-microbe interaction in Rhizosphere must increase before we can presume that utilization of PGPR as biofertilizers will determine a sustainable promotion of host plants growth. Combinations of beneficial bacterial strains that interact synergistically are currently being devised and numerous recent studies show a promising trend in the field of inoculation technology. PGPR are excellent model systems which can provide the biotechnologist with novel genetic constituents and bioactive chemicals having diverse uses in agriculture and environmental sustainability.

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