Plant-Growth-Promoting Rhizobacteria

H Antoun, Université Laval, Québec, QC, Canada

This article is a revision of the previous edition article by H Antoun, J Kloepper, volume 3, pp 1477–1480, © 2001, Elsevier Inc.

Glossary

Diazotroph A N_2-fixing microorganism.
Mycorrhiza Symbiotic association between higher plants and specific fungi.
Mycorrhizosphere Soil attached to the roots of a mycorrhizal plant.
Rhizobacteria Rhizosphere-competent bacteria.
Rhizoplane Plant material of the root surface in direct contact with the rhizosphere.
Rhizosphere Soil closely attached to plant roots.
Rhiz From the Greek, rhiza, for root.

The Rhizosphere

Intensive interactions take place in the root zone between plant, soil, and microorganisms. Plants take up most of their requirements in nutrients and water from the roots and they release a large number of low-molecular-weight water-soluble exudates such as amino acids, hormones, organic acids, sugars, and vitamins. At the beginning of the twentieth century, the term 'rhizosphere' was proposed to indicate soil strongly attached to the roots. In addition to root exudates, the rhizosphere is in contact with other plant-derived products of high or low molecular weight, which contribute nutrients to the richness of this ecological niche.

The Mycorrhizosphere

The root–soil zone is very complex and has generated many definitions for the different ecological niches involved. The rhizoplane is the plant root surface. Endophytes are microorganisms colonizing the interior of plant tissues, including roots. The majority (80%) of land plants form symbiotic associations with mycorrhizae and these symbiotic fungi can change the physiology of plants and their root exudates, and consequently they modify the structure of associated root bacterial communities. Therefore, the term 'mycorrhizosphere' refers to the soil associated to mycorrhizal plant roots, and it includes in addition to the rhizoplane and the rhizosphere, the hyphosphere (soil surrounding the fungal hyphae).

The Rhizosphere Effect on Soil Microorganisms

The importance and activity of soil microorganisms are influenced by two important limiting factors: carbon and water. The rhizosphere (R) is a niche containing substantially more nutrients than the nonrhizosphere (S) soil. The R/S ratio of the numbers of microorganisms is used to illustrate how the rhizosphere affects the different groups of microorganisms. In general, total microbial counts are found to be increased 10- to 50-fold in the rhizosphere. However, R/S values ranging from 100 to more than 1000 can be observed for some specific groups of soil microorganisms like denitrifiers. Bacteria are the most abundant group of microorganisms in the rhizosphere. Rhizosphere microorganisms are soil borne, but they may arise from seed-borne populations, which survive storage and germination.

Effect of Rhizobacteria on Plant Growth

Rhizobacteria are bacteria that are rhizosphere competent. They compete for nutrients and occupy and persist in the ecological niches found on plant roots.

Some rhizobacteria are endophytes able to enter plant roots. Apart from plant pathogens, rhizobacteria can have neutral, deleterious, or beneficial effects on plant growth. Deleterious microorganisms are not parasitic, but they limit plant growth by altering water or mineral ion uptake or the activity of plant growth substances.

Plant Growth-Promoting Rhizobacteria

Plant growth-promoting rhizobacteria (PGPR) are a very small portion of rhizobacteria (2–5%) that promote plant growth. The term 'PGPR' was elaborated in 1978 by Kloepper and Schroth and used to designate the rhizobacteria showing significant plant growth promotion, as shown with the substantial increases in fresh matter yield obtained with inoculated radishes. Rarely, PGPR can be present in high numbers, as in some suppressive soils. Beneficial symbiotic bacteria like *Rhizobium*, which form N_2-fixing nodules with legumes, are considered PGPR if they stimulate the growth of other nonlegume plants without modifying the roots' normal appearance.

Species of PGPR

Most PGPR have been found among Gram-negative bacteria because they are easily isolated and genetic tools for their study are readily available. The first isolated PGPR were fluorescent pseudomonads; however, nonfluorescent pseudomonads, *Burkholderia*, *Arthrobacter*, *Serratia*, and *Achromobacter* also stimulate plant growth. Some strains of *Rhizobium*, the symbiotic partner of legumes, can behave like other PGPR with nonleguminous plants such as corn, lettuce, radishes, and rice. However, like *Azospirillum* spp. and *Azotobacter* spp., also diazotrophs, the beneficial effect of *Rhizobium* on nonlegumes does not result from their ability to fix N_2, but rather from their ability to produce plant hormones. Gram-positive bacteria are less documented and should not be overlooked since many are able to sporulate, as they offer a practical advantage for the development of PGPR inoculants' retaining viability when dried. Most commercial products with PGPR are based on strains of *Bacillus* and related genera. Isolates of *Brevibacterium*, *Corynebacterium*, *Micrococcus*, *Paenibacillus*, and *Sarcina* have been reported as PGPR.

Mycorrhiza and PGPR

Since mycorrhiza are ubiquitous, most economically important plants have a mycorrhizosphere. Mycorrhiza helper bacteria (MHB) are mycorrhiza-associated bacteria promoting the establishment and functioning of the symbiosis. MHB that promote promoting plant growth and health are by definition PGPR.

Mechanisms of Growth Promotion by PGPR

Plant Growth Promotion

The beneficial effects of PGPR result from improvement of plant growth and health and can be evidenced by increases in seedling emergence, nutrients uptake, vigor, root system development, and yield. PGPR promote plant growth by one or more of direct or indirect mechanisms. Production of plant hormones, improvement of plant nutrition, and degradation of xenobiotics in the root environment are examples of direct mechanisms. PGPR can indirectly enhance plant growth by eliminating pathogens or by inducing plant defense responses. Many PGPR act by more than one mechanism. Early studies with PGPR were performed with root plants such as potato and sugar beet. Presently, PGPR are studied with many crop plants, horticultural crops, and cultivated trees.

Direct Plant Growth Promotion

Auxins, cytokinins, gibberellins, ethylene, and abscisic acid are plant hormones produced by PGPR. Indole-3-acetic acid (IAA) is the most abundant auxin and its biosynthetic pathways in bacteria are well characterized. Inoculation of maize with IAA-producing *Pseudomonas* and *Acinetobacter* strains promotes root elongation and lateral root production. Inoculation of young maize plants with these PGPR produces an effect comparable to the application of IAA: higher root dry matter production and higher concentrations of Ca, K, Mg, P, Fe, and Zn found in the roots. Inoculation of maize with *Azospirillum brasilence* and rice with *A. lipoferum* enhanced the uptake of phosphate, nitrate, and ammonium. When present at high concentration, IAA can increase the activity of 1-aminocyclopropane-1-carboxylic acid (ACC) synthase, thus increasing the concentration of ACC, the precursor of ethylene. In response to stresses caused by high concentrations of salts or heavy metals, or by pathogen attacks, plants produce a high concentration of ethylene, causing an adverse effect on plant growth. Therefore, PGPR-producing ACC deaminase, the enzyme degrading ACC, will reduce ethylene levels and will mitigate many plant stresses. Ethylene is required for the induction of systemic resistance in plants and it is involved in plant defense pathways induced in response to pathogen infection. PGPR that produce giberellins stimulate root growth and increase root hair density, improving water and nutrient uptake.

Some PGPR can improve plant P nutrition by producing organic acids or protons (H^+ ions), which mobilize P from sparingly soluble inorganic phosphates or phosphate rock. Production of phosphatase enzymes mobilizes organic P. A synergistic effect between mycorrhiza and PGPR on P mobilization is frequently observed.

Colonization of barley roots with a strain of *Burkholderia cepacia* that degrades the herbicide 2,4-dichlorophenoxyacetic acid (2,4-D) protects the plant in an inhibitory contaminated soil.

Beneficial Effect on Symbioses

Pea, lentil, bean, and soybean show increased nodulation and N_2-fixation increase when co-inoculated with PGPR (*Bacillus*, *Pseudomonas*, and *Serratia* spp.). Mechanisms whereby MHB help the establishment of mycorrhiza might be by the production of growth factors stimulating mycelial growth and spore germination, or by increasing root branching that enhances root colonization. Another such mechanism is exemplified by the ACC deaminase producing MHB *Pseudomonas putida* UW4, which reduces ethylene production and increases the colonization of cucumber with the mycorrhiza *Gigaspora rosea*.

Biological Control

Some PGPR exhibit biocontrol activity against a broad spectrum of plant pathogens including bacteria, fungi, nematodes, viruses, and insects. Production of antibiotics, cyanide, lytic enzymes, and siderophores; interference with fungal pathogenesis factors; and induced systemic resistance are mechanisms of action by PGPR that effect biocontrol. Production of antimicrobial compounds by *Pseudomonas* and *Bacillus* species has been widely studied, and their mechanisms of action were established by showing that production-impaired mutants are less suppressive. 2,4-Diacetylphloroglucocinol, phenazine-1--carboxylic acid, pyoluteorin, and pyrrolnitrin are examples of antibiotics produced by Gram-negative fluorescent pseudomonads. Gram-positive bacilli produce several antibiotics, such as iturin A, macrolactin A, zwittermicin A, and Kanosamine.

Under iron-limited conditions, some PGPR produce siderophores with very high affinity to ferric iron; for example, fluorescent *Pseudomonas* PGPR strains produce the siderophores pseudobactins. By binding Fe(III), siderophores immobilize this essential element, inhibiting the growth of deleterious and soil-borne bacterial or fungal pathogens unable to use this iron complex. Effective PGPR produce siderophores-specific membrane protein receptors that allow them to use iron. In addition to its own siderophore, a strain of PGPR can use siderophores produced by other rhizobacteria. Biological control activity mediated by siderophores is nullified by the addition of soluble iron.

Strain CHAO of *Pseudomonas fluorescens* is an interesting model strain that produces several antifungal antibiotics such as 2,4-diacetyl phloroglucinol, involved in the suppression of black root rot of tobacco and of wheat take-all, and pyoluteorin that suppresses *Pythium*-induced disease of cress. Strong correlations were observed between the ability of fluorescent pseudomonads to produce hydrogen cyanide and to suppress infection of pea seeds by *Pythium ultimum*.

Biocontrol strains of *Burkholderia* spp. degrade fusaric acid, a pathogenicity factor of *Fusarium oxysporum*, resulting in plant protection. Similarly, degradation of the quorum-sensing molecule *N*-acylhomoserine lactone (AHL) by PGPR can protect the plant against *Erwinia carotovora*, since AHL is necessary for the production of cell wall-degrading enzymes by this pathogen.

The biological control activity of some PGPR against fungi is associated with bacterial production of lytic enzymes such as chitinases, beta-1,3-glucanases, or proteases. This mechanism, used successfully in the biological control of *Pythium* and *Fusarium* spp., is found in *Bacillus*, *Serratia*, and *Streptomyces* species and is referred to as parasitism.

PGPR indirectly promote plant health by induced systemic resistance (ISR). In absence of pathogens, the presence of PGPR induces plant defense mechanisms against organisms causing foliar diseases. ISR involves plant structural changes such as the formation of new barriers and increased activity of lytic enzymes. PGPR-mediated ISR reduces the incidence of diseases caused by bacteria, fungi, insects, nematodes, and viruses. ISR is induced by many bacterial components such as lipopolysaccharides (LPS), flagella, salicylic acid, siderophores, cyclic lipopeptides, AHL, acetoin, and 2,3-butanediol.

Future Prospects

PGPR are tools *par excellence* for the sustainable development in agriculture and forestry. Several reports show that PGPR successfully replace man-made pesticides and reduce application rates of chemical fertilizers. Although PGPR have been studied as free-swimming cells, when introduced by inoculation they attach to roots, mycorrhizal hyphae, and soil particles to form biofilms. Future research should be aimed at the elucidation of the importance and nature of the biofilms formed in relation to their beneficial or deleterious effect on plant growth.

See also: Bacteria; Biofilms; Plant Hormones; Rhizobium; Symbionts, Genetics of.

Further Reading

Avis TJ, Gravel V, Antoun H, and Tweddell R (2008) Multifaceted beneficial effects of rhizosphere microorganisms on plant health and productivity. *Soil Biology and Biochemistry* 40: 1733–1740.

Bonfante P and Anca I-A (2009) Plants, mycorrhizal fungi, and bacteria: A network of interaction. *Annual Review of Microbiology* 63: 363–383.

Compant S, Clément C, and Sessitsch A (2010) Plant growth-promoting bacteria in the rhizo- and endosphere of plants: Their role, colonization, mechanisms involved and prospects for utilization. *Soil Biology and Biochemistry* 42: 669–678.

Francis I, Holsters M, and Vereecke D (2010) The Gram positive side of plant–microbe interactions. *Environmental Microbiology* 12: 1–12.

Frey-Klett P, Garbaye J, and Tarkka M (2007) The mycorrhiza helper bacteria revisited. *New Phytologist* 176: 22–36.

Haas D and Défago G (2005) Biological control of soil-borne pathogens by fluorescent pseudomonas. *Nature Reviews Microbiology* 3: 307–319.

Lugtenberg B and Kamilova F (2009) Plant growth-promoting rhizobacteria. *Annual Review of Microbiology* 63: 541–556.

Rudrappa T, Biedrzycki ML, and Bais HP (2008) Causes and consequences of plant-associated biofilms. *FEMS Microbiology Ecology* 64: 153–166.

Spaepen S, Vanderleyden J, and Okon Y (2009) Plant growth promoting actions of rhizobacteria. In: Van Loom LC (ed.) *Plant Innate Immunity*, ch. 7. *Advances in Botanical Research* 51: 283–320.

Yang J, Kloepper JW, and Ryu C-M (2009) Rhizosphere bacteria help plants tolerate abiotic stress. *Trends in Plant Science* 14: 1–4.