Plant Growth Promoting Microorganisms: Plant Microbe Interactions

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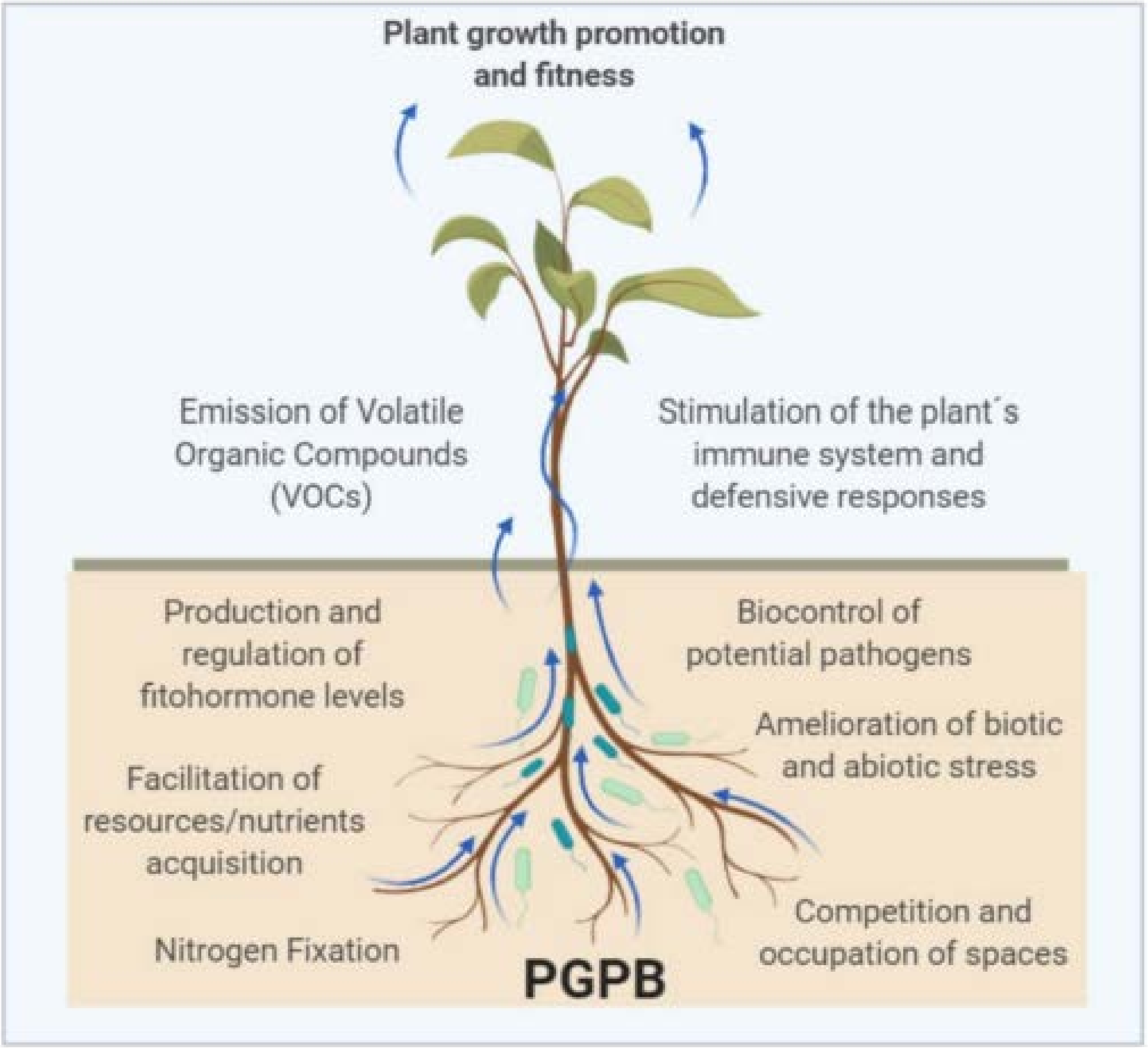
Plant-Associated Bacteria

- A plant growing under field conditions is not an individual.
- It is a complex community with subtle and relatively constant partner relationships.
- A well-structured and regulated community of microorganisms is always associated with the plant. This community is the phytomicrobiome.
- The phytomicrobiome plus the plant is the holobiont.
- There are elements (including bacteria and fungi) of the phytomicrobiome associated with all major plant structures (flowers, fruits, stems, leaves, and roots).
- However, conditions vary substantially among these structures, leading to specialized microbial populations inhabiting each one.
- All these plant-associated bacteria might be able to exert beneficial mechanisms, such as direct and indirect (biocontrol) plant growth promotion are known as **plant growth promoting bacteria (PGPB)**.
- The microbial community associated with the roots (the rhizomicrobiome), is the most populous and elaborate of all those associated with higher plants.
- In the soil, there is a gradient of intimacy between plant roots and microbes extending away from the plant root: the degree of plant influence over the microbial community increases nearer the root surface.

Beneficial mechanisms exerted by plant growth-promoting bacteria (PGPB) to stimulate healthy plant growth and fitness



Plant Growth Promoting Bacteria

- The use of microbial based agricultural inputs has a long history, beginning with broad-scale rhizobial inoculation of legumes in the early 20th century.
- More recently, strains of *Bacillus, Pseudomonas, Glomus*, and others have been commercialized.
- The use of bacterial taxa in plant production has been reviewed previously for *Bacillus, Pseudomonas, Actinobacteria*, and *Lactobacillus*.
- In addition, *Acetobacter, Azospirillum, Paenibacillus, Serratia, Burkholderia, Herbaspirillum*, and *Rhodococcus* have also been shown to enhance crop production.

Mechanisms of actions of PGPB

- **Direct Mechanisms:** The direct mechanisms of plant growth promotion include the facilitation of nutrient acquisition and the synthesis of hormones.
- One of the main problems that plants face in acquiring nutrients is the poor solubility of the elements in the soil.
- For example, phosphorus is scarce in many soils worldwide, besides being in insoluble forms, limiting its use by plants.
- Plants generally obtain soluble phosphorus in two forms, monobasic and dibasic.
- **Phosphorus** is present in the soil as inorganic minerals, such as apatite, or as one of the several organic forms, including inositol phosphate, phosphomonoesters, and phosphotriesters.
- Inorganic phosphorus is applied in the field as a chemical fertilizer, along with other elements such as nitrogen. However, as phosphorus is mostly insoluble, the plant does not use it and it leaches, contaminating the ground water reserves.

Direct Plant Growth Promotion

- Therefore, the use of phosphate solubilizing PGPB, including genera such as *Achromobacter, Agrobacterium, Bacillus, Enterobacter, Erwinia, Flavobacterium, Gluconacetobacter, Mycobacterium, Pseudomonas* and *Serratia*, play a fundamental role in solubilizing insoluble forms of phosphorus, mainly through mechanisms such as the production of acid phosphatases, which help to mineralize organic phosphorus in the soil.
- The production of organic acids such as gluconic acid and citric acid by PGPB help in the solubilization of phosphorus, in such a way that, when plants acquire these solubilized or mineralized molecules, their growth and production can be stimulated.
- Moreover, production of organic and inorganic acids such as citrate, oxalate, acetate, sulfuric acid, carbonic acid and nitric acids by PGPB, also stimulates the solubilization of other elements, such as **zinc** and **potassium**, which are essential for soil fertility and crop improvement

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- **Iron:** Siderophores are iron-chelating compounds secreted by bacteria that reduce iron (Fe^{3+} to Fe^{2+}) intra and intercellularly and can be used either by the plant or the endophyte. Siderophores have a relevant function when Fe is scarce in the environment.
- Characteristically, *Pseudomonas* species fluorescence is due to their different kinds of siderophores, such as pyochelin, pseudobactin, and pyoverdine.
- Several studies have shown that microbial siderophores can directly increase plant growth through the improvement in iron acquisition.
- For example, *P. fluorescens* strain C7 produces siderophores of the pyoverdine type, which forms a pyoverdine-Fe complex.
- This complex may be taken up by plant *Arabidopsis thaliana* and increase its growth.
- Microbial siderophores are synthesized by various taxa and may participate through indirect mechanisms in plant growth.

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- **Nitrogen (N):** is another essential element for the development and production of fruits and seeds in plants of agricultural interest.
- Leguminous plants may symbiotically interact with soil bacteria collectively known as rhizobia, which include the genera *Bradyrhizobium, Sinorhizobium/Ensifer, Mesorhizobium, Rhizobium, Azorhizobium, Neorhizobium*, and *Pararhizobium*.
- These are free-living bacteria (diazotrophic) that may penetrate plant tissues through the exchange of chemical signals and form nodules.
- Nodules are globular or cylindrical structures where rhizobial endophytes reside and are capable of fixing atmospheric nitrogen and converting it into ammonia, an assimilable form of nitrogen for the plant.
- Some non-nitrogen-fixing bacteria, such as *Pseudomonas*, may stimulate the legume-rhizobia symbiosis in addition to increasing levels of nitrogen fixation, thus improving plant growth and nutrition.
- For example, the high activity levels of the enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase detected in *Pseudomonas* are essential to enhance the nodulation process in rhizobia, showing that a beneficial interaction between bacteria may also benefit the plant.

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- The production of phytohormones and other diffusible or volatile compounds that modulate plant growth is a relevant factor for potential endophytes that are candidates for being used as **biostimulant** products in agricultural crops.
- **Phytohormones** are key players in regulating plant growth and development.
- They also function as molecular signals in response to environmental factors that otherwise limit plant growth or become lethal when uncontrolled.
- Many rhizosphere bacteria are known to excrete hormones for root uptake or manipulate hormone balance in the plants to boost growth and stress response.
- PGPR that produce auxins have been shown to elicit transcriptional changes in hormone, defense-related, and cell wall related genes, induce longer roots, increase root biomass and decrease stomata size and density, and activate auxin response genes that enhance plant growth.

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- Some strains of PGPR can promote relatively large amounts of gibberellins, leading to enhanced plant shoot growth.
- Interactions of these hormones with auxins can alter root architecture.
- Production of cytokinins by PGPR can also lead to enhanced root exudate production by the plant potentially increasing the presence of PGPR associated with the plant.
- Ethylene is a gaseous hormone, active at extremely low concentrations (0.05 mL L^{-1}) and is a "stress hormone," as illustrated by its concentration spiking during various abiotic and biotic stresses.
- Accumulation of ethylene in response to stress may increase plant tolerance or exacerbate stress-response symptoms and senescence.
- PGPR often provides greater growth stimulation under stressful conditions, for instance, under drought stress.
- Many studies have shown enhanced stress tolerance in plants through inoculation with PGPR that produce ACC deaminase.
- PGPR secrete 1-aminocyclopropane-1-carboxylase (ACC) deaminase which reduces ethylene production in plants. This appears to occur since PGPR are able to keep ethylene levels from reaching levels sufficient to reduce plant growth.
- A wide range of VOCs produced by bacteria can improve stress tolerance and/or stimulate growth in plants. For example, acetoin, 2,3-butanediol, and N,N-dimethylhexadecylamine.

Indirect Plant Growth Promotion

- Indirect mechanisms include antagonism of PGPB towards potential phytopathogens.
- Restricting the growth or eliminating pathogens is an indirect mechanism for PGPB to promote the growth and health of the plant.
- PGPB contain an entire arsenal of compounds and enzymes that have the ability to restrict or eliminate pathogens.
- **Siderophores** produced by bacteria of the genus *Pseudomonas* have the ability to chelate the Fe available from the medium, restricting it to pathogens.
- **Cell wall degrading eenzymes:** such as chitinases, cellulases, and β-1,3-glucanases that degrade the fungal cell wall.
- Chitinase degrades chitin, an insoluble linear polymer of β-1,4-N-acetyl-glucosamine, known to be the major component of the fungal cell walls.
- β-1,3-glucanase, another cell wall carbohydrate; protease, which can degrade cell wall proteins; and lipase, which can degrade some of the cell wall-associated lipid, all of which can to some extent individually lyse fungal cells.

… Indirect Plant Growth Promotion

- **Antibiotics:** The major mechanism that used by PGPB to counter deleterious effects of phytopathogens is the synthesis of one or more antibiotics.
- Many antibiotics have been derived from bacteria of the genera *Bacillus* and *Pseudomonas*.
- They produce a variety of metabolites which serve as antifungal, antibacterial, antihelminthic, antiviral, antimicrobial, phytotoxic, antioxidant, cytotoxic, and antitumor agents.
- For *Bacillus*, they are either derived from the ribosome or the non-ribosomal peptide and/ or polyketide synthetases (NRPSs/PKS).
- Examples include Tas A, sublancin, subtilosin, bacilysin, chlorotetain, subtilin, bacillaene, surfactin, iturin, and fengycin.
- While from *Pseudomonas* we have Ecomycins, 2,4-Diacetyl Phloroglucinol (DAPG), Pseudomonic acid, Phenazine-1-carboxylic acid (PCA), Pyoluteorin, Pyrrolnitrin, OomycinA, Cepaciamide A, Viscosinamide, Butyrolactones, Zwittermycin A, Aerugine, Azomycin, Rhamnolipids, Cepafungins, Kanosamine, and Karalicin

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- **Competition:** In addition to mechanisms where a biocontrol PGPB produces substances that are inhibitory to phytopathogens per se, it is possible for some biocontrol PGPB to outcompete the phytopathogens, either for nutrients or for binding sites on the plant root.
- Such competition can act to limit the binding of the phytopathogen to the plant thereby making it difficult for it to proliferate.
- **HCN** toxicity is effected in its ability to inhibit cytochrome c oxidase as well as other important metalloenzymes.
- Many bacterial genera such as *Rhizobium, Pseudomonas, Alcaligenes, Bacillus*, and *Aeromonas* have shown to be HCN producers.
- **Induced systemic resistance:** ISR is a process in which nonpathogenic microbes, including a number of PGPB, alleviate the deleterious effects of plant pathogens by activating a resistance mechanism in the plants.
- Pre-treatment of plants with an appropriate PGPB can prime the plant to react faster and more strongly to a subsequent pathogen attack by inducing plant defense mechanisms.

… **Indirect Plant Growth Promotion**

- ISR does not target specific pathogens but rather primes the plant against a range of different pathogens, and it is not only expressed at the site of induction only.
- ISR confers a high level of protection which is controlled by a network of coordinated signaling pathways which are dominated and majorly regulated by plant hormones sharing signaling components.
- The production of other volatile compounds such as ethylene, methyl salicylate, and methyl jasmonate may induce and control plant defense responses.
- *Bacillus* sp. JS was shown to cause ISR through an upregulation of the PR-2 and PR-3 genes which encode β-1,3-glucanase and chitinase respectively.

… Indirect Plant Growth Promotion

- **Quorum quenching:** In the environment, bacterial cells use the mechanism of quorum sensing to detect the presence of similar (as well as different) types of bacteria.
- With growing bacterial cells, once they have attained a certain critical cell density, the bacteria “sense” the cell density (through the production of chemical signals) and start to alter their metabolism by turning on different sets of genes, so that similar bacteria that are proximal to one another may begin acting in a coordinate manner.
- Disrupting this quorum sensing (i.e. signaling amongst pathogens) can thwart the pathogen from becoming increasingly virulent and prevent it from inhibiting plant growth.
- PGPB that produces an enzyme called a lactonase that degrades the pathogen-produced autoinducer and pretreat plant seedlings (when they are most sensitive to many pathogens) with this PGPB, especially in situations where a particular bacterial pathogen is known to be particularly problematic.
- While this is a clever strategy that has been successful in lab, it has not yet been successfully tested in field.

… **Indirect Plant Growth Promotion**

- **Bacteriophages:** Some bacterial phytopathogens may be lysed by specific bacteriophages, or bacterial viruses.
- For this approach to work, the target bacterial phytopathogen must be unequivocally identified down to the strain level.
- Subsequently, it is possible to isolate and thoroughly characterize several different bacteriophages that can lyse only the target pathogen without affecting any other bacterial strains.
- To kill the target bacterial phytopathogen, the bacteriophages are sprayed onto an infected plant as a mixture of two or three different bacteriophage strains all directed against the targeted bacterial pathogen.
- At the present time, a few bacteriophage-based biocontrol agents have been licensed for use, e.g. for the bacterial pathogen *Xanthomonas campestris* pv. *vesicatoria* which causes bacterial spot of tomatoes and peppers, *Pseudomonas syringae* pv. *actinidae* which causes canker disease in kiwi fruit, and *Pseudomonas syringae* pv. *tomato*, which causes bacterial speck on tomatoes