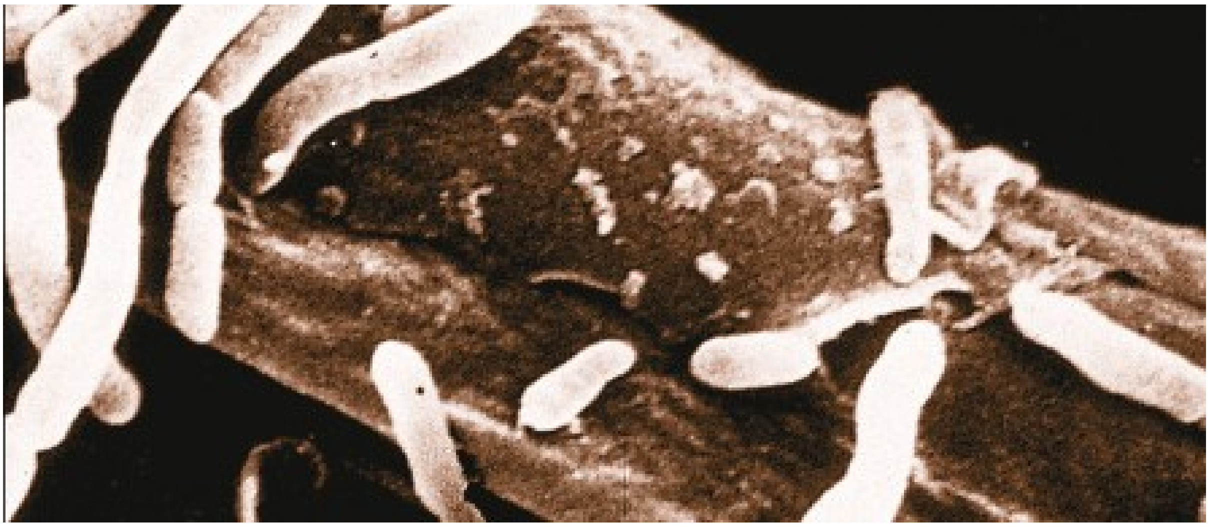
Plant Growth-Promoting Bacteria

Daddy: why are the roots of plants coated with bacteria?



Bernard R. Glick

Department of Biology, University of Waterloo, Waterloo, Ontario, Canada N2L 3G1

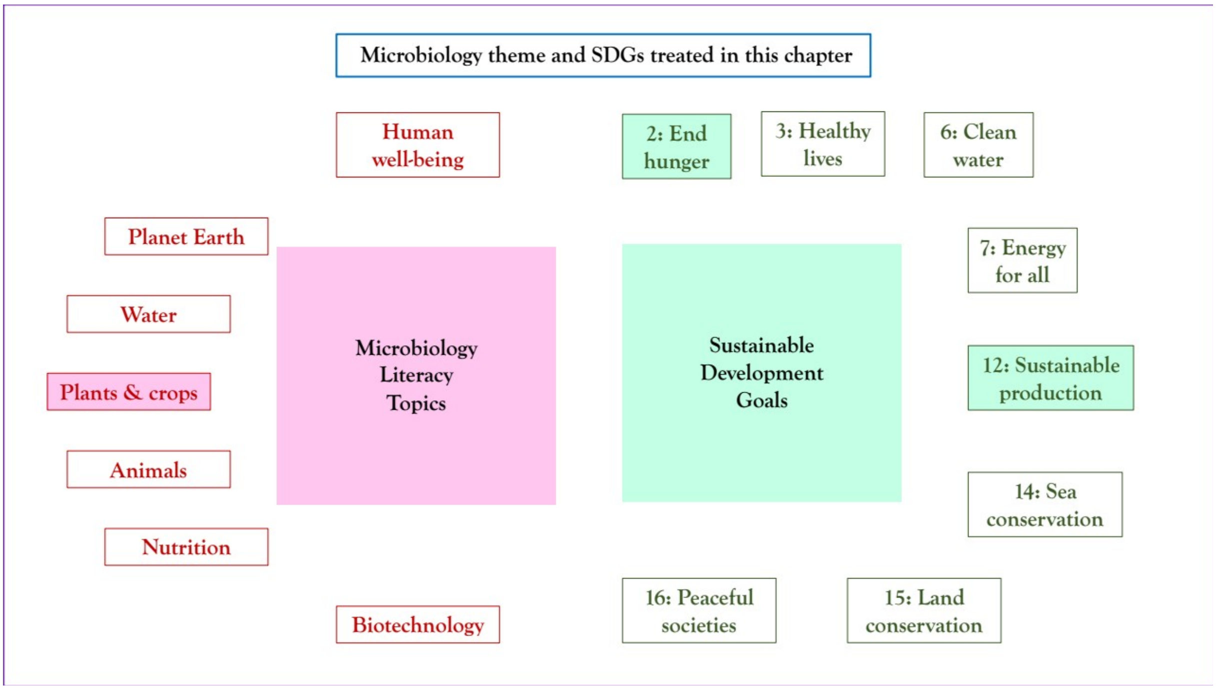
Plant Growth-Promoting Bacteria

Storyline

The population of the world is currently approaching 8 billion people and it is continuing to grow. This puts a tremendous stress on the world's food supply. In addition, it has been estimated that as a consequence of insufficient or inadequate food, currently nearly 1 billion of the world's people are malnourished and this in turn contributes to deaths of about 3 million children a year. It is therefore necessary to find ways to feed this very large and growing global population both now and in the future. At the same time that we have a need for more and more food to feed all of the people in the world, we continue to pollute the air, water and soil, all of which makes it even more difficult to produce crop plants.

There probably isn't just one simple solution to the problem of adequately feeding all of the people in the world both now and in the future. However, there are a number of things that we can do that should increase the global food supply. For a start, we need to stop polluting the environment so that available farmland remains intact and we do not make the situation any worse than it already is. Second, we need to be able to deliver food more efficiently from where it is produced to where it is consumed, thereby decreasing a lot of food spoilage and wastage. Third, in the more affluent countries of world, we need to decrease portion size in restaurants and the overconsumption of meat (which uses much more in terms of resources in their production than does plant protein). Fourth, we need to increase the agricultural productivity of marginal land. Fifth, we need to embrace the more widespread use of transgenic plants which promises to produce crops with increased yields, better nutritional content, and greater resistance to disease and various pests, including insects, viruses, fungi, nematodes and pathogenic bacteria. Sixth, we need to decrease the widespread use of agricultural chemicals (including chemical fertilizers, pesticides and herbicides) and instead embrace the much more widespread use of naturally-occurring plant growth-promoting bacteria.

The Microbiology and Societal Context

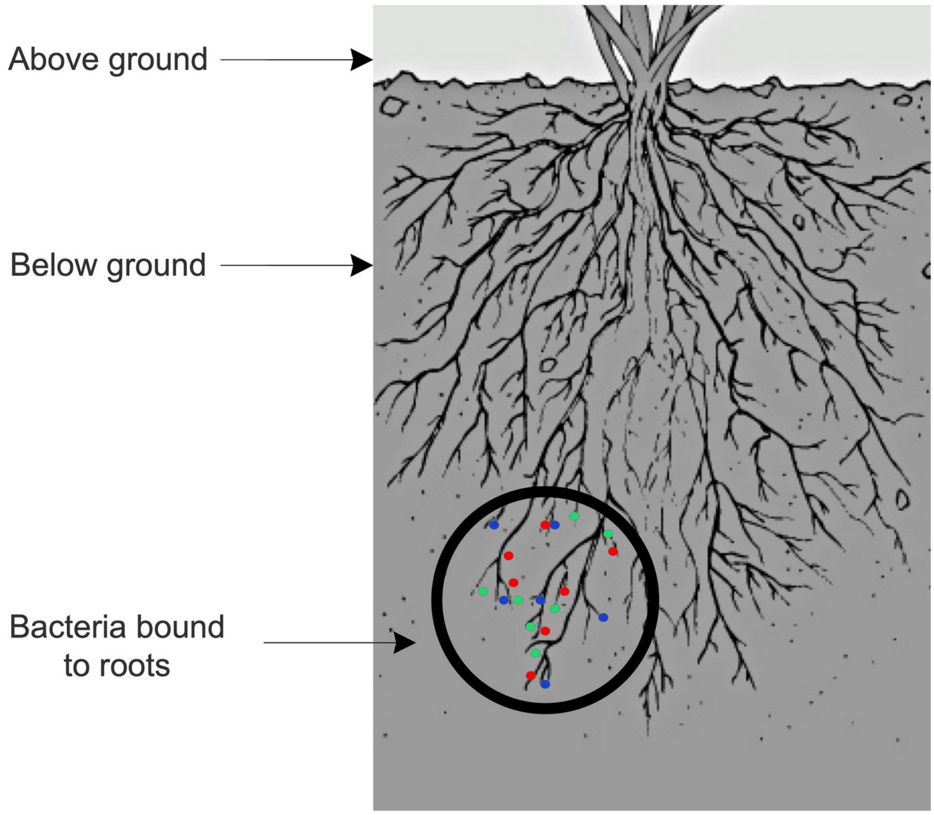


The microbiology: plant growth-promoting bacteria in agriculture and environmental cleanup; pollution; eutrophication and toxic algal blooms; microbial greenhouse gas production;. *And, peripherally for completeness of the storyline*: feeding the world; organic agriculture. *Sustainability issues:* health; food and energy, economy and employment; environmental pollution; global warming.

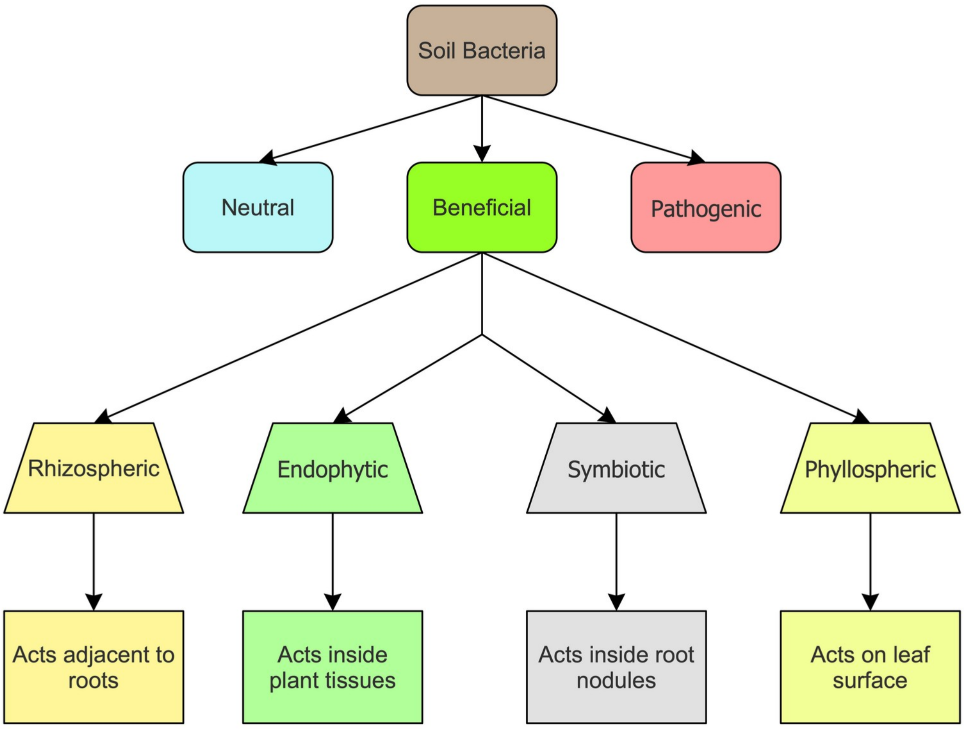
Plant Growth-Promoting Bacteria: the Microbiology

1. ***Plant Growth-Promoting Bacteria.*** Soils worldwide contain an enormous number of microorganisms with some scientists estimating that there may be up to 100 million organisms in just one gram of some soils, with approximately 90-95% of those organisms being bacteria. Of course, there really is not anything that can be described as a typical soil, especially given that soils vary enormously from one location to another (different soils vary in their mineral content, their chemical composition, their amount of water and their pH, with these different conditions favoring the growth of different soil bacteria). Typically, the concentration of soil bacteria is much greater (around 10- to 1000-fold) around the roots of plants than in the rest of the (bulk) soil. This is because plant roots leak (or exude) many small molecules into the soil. These small molecules, which include a variety of sugars and organic acids, act as a food source for the bacteria in the soil.

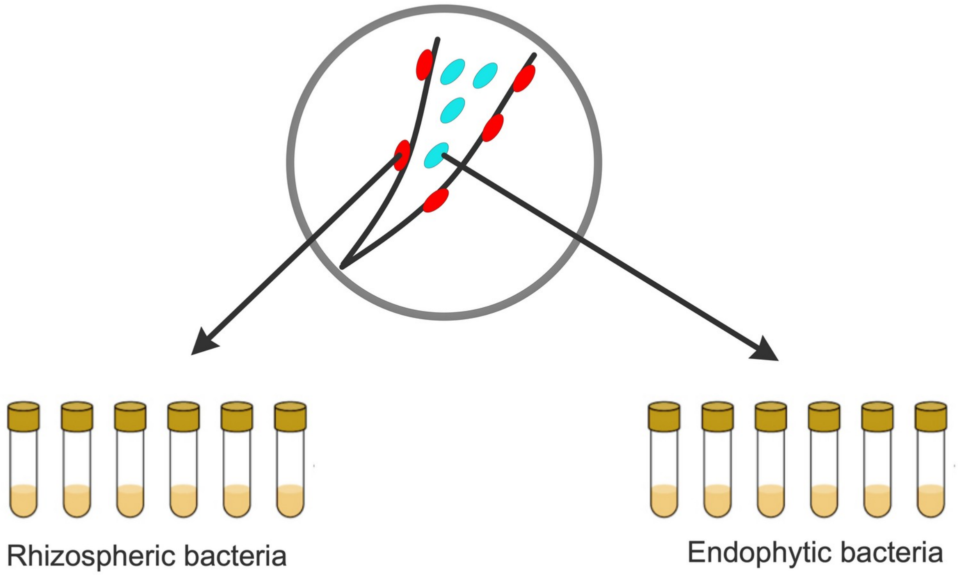
The interaction between bacteria and plants may be beneficial, harmful or neutral for the growth and development of the plant. Beneficial bacteria are commonly called plant growth-promoting bacteria. Bacteria that are harmful to plants are considered to be phytopathogens (and are the causes of various plant diseases). The figure below shows a schematic representation of a portion of a plant's roots with a number of bacteria that are found very close to the roots or are bound to the roots (phytopathogens are shown in red; plant growth-promoting bacteria are shown in green; and neutral bacteria are shown in blue).



Plant growth-promoting bacteria that are found primarily around plant roots are said to be rhizospheric (with rhizo meaning root). Plant growth-promoting bacteria that can exist within plant tissues (generally including roots but often also including shoots and leaves) and also benefit plant growth, are termed endophytic. Those bacteria that are found on the surface of green plant tissues, such as leaves, are called phyllospheric. In addition, some endophytic bacteria that bind to and enter into the root tissues of only a very limited number of plants are sometimes called symbiotic bacteria. Symbiotic bacteria generally enter plant roots and (in cooperation with the plant) form nodules where these bacteria subsequently reside. The figure below schematically shows the different types of soil bacteria with an emphasis on the beneficial or plant growth-promoting bacteria and the functioning of these beneficial bacteria.



Scientists have figured out how to isolate many (but not all) plant growth-promoting bacteria in the laboratory and then grow these beneficial bacteria in relatively large amounts (relatively inexpensively). Once the isolated beneficial bacteria have been characterized biochemically and physiologically in a controlled laboratory environment, they can then be tested in the laboratory to ensure that they can effectively promote various aspects of plant growth (such as the rate of seed germination, the size of the plants, both root and shoots, and the nutritional content of the plants. Following successful testing of newly isolated and characterized strains, the laboratory-grown plant growth-promoting bacteria may then be added to plant seedlings or plant seeds in the field so that plants can benefit from some of the traits that the beneficial bacteria possess. In the figure below we can see the localization of rhizospheric bacteria (in red) and endophytic bacteria (in blue) that are found either on or inside of a plant root, followed by their subsequent isolation. Interestingly, regardless of whether plant growth-promoting bacteria are located on the outside or the inside of a plant root, for the most part these bacteria generally have very similar effects on plant growth and development. This is most likely due to the fact that regardless of their location on the plant, different plant growth-promoting bacteria employ very similar mechanisms to facilitate plant growth.

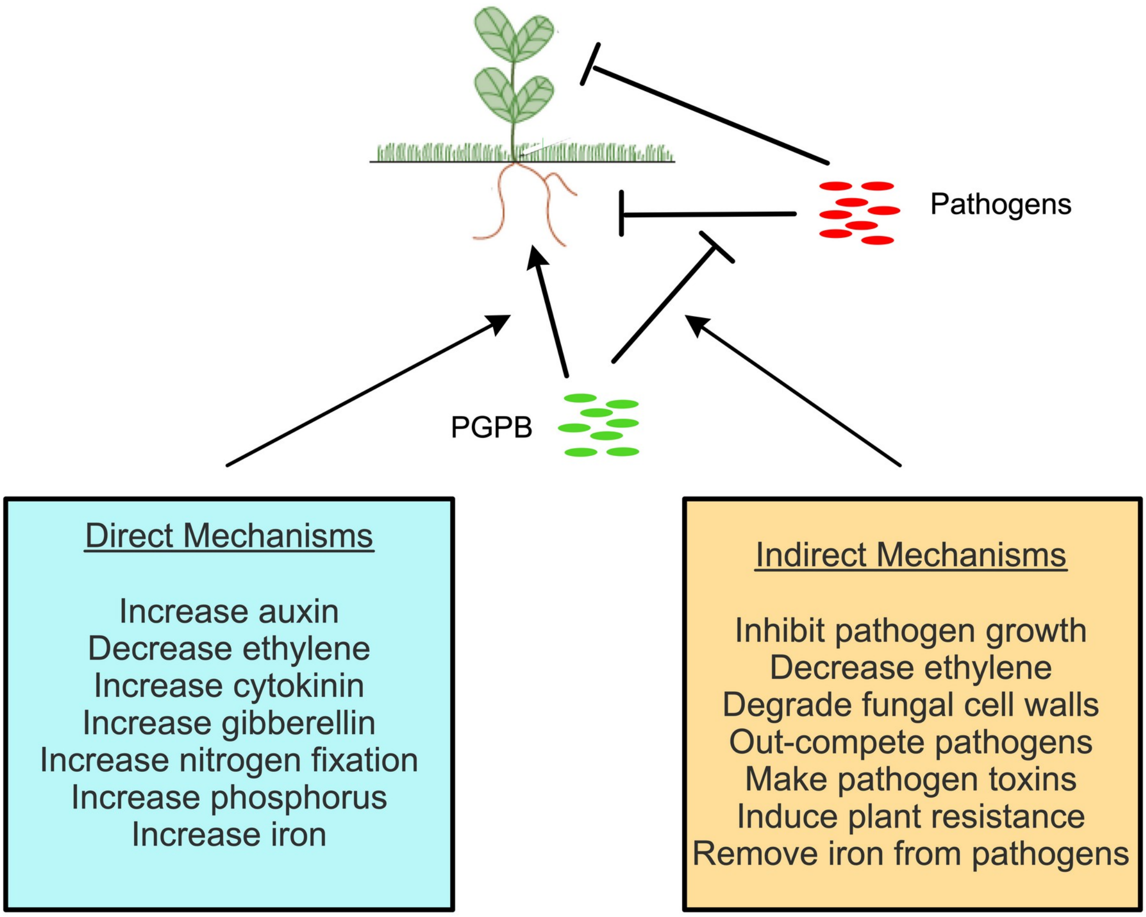


2. ***Effects of plant growth-promoting bacteria on plants.*** Treating growing plants with plant growth-promoting bacteria can have a number of different effects. Some of these positive effects include: (1) the added bacteria may increase the yield of a plant; (2) the bacteria may help a plant to increase its levels of one or more essential nutrients such as nitrogen, phosphorus or iron; (3) the bacteria may help to increase the length of the plant roots or shoots thereby increasing the amount of water and nutrients that plants can extract from soil (roots) and the ability of the plant to capture energy from the sun (shoots) and therefore increase the yield of the plant; (4) the bacteria may increase the number of plant seeds that are formed and the percentage of seeds that germinate; (5) different bacteria may protect plants against a wide range of pathogens and pest including insects, fungi, nematodes and pathogenic bacteria; (6) some bacteria are able to protect plants against a number of different abiotic (non-biological) stresses such as high and low temperatures, drought, flooding, the presence of high levels of salt, extremes of pH (acidity and alkalinity) and the presence of toxic chemicals in the soil; and (7) the presence of plant growth-promoting bacteria can sometimes increase the amount of fruit that some plants produce. Also, different bacteria can impact various plants in different ways with the growth of some plants being more likely to be positively affected by particular strains than the growth of other plants. Moreover, different plant growth-promoting bacteria employ different mechanisms of growth promotion and, in addition they use these mechanisms to different extents (see the next section).

3. ***Mechanisms employed by plant growth-promoting bacteria.***_The mechanisms that plant growth-promoting bacteria use may be divided into two main categories, i.e. direct and indirect promotion of plant growth (see figure below). Direct promotion of plant growth is when the added bacteria provide something directly to the plant to facilitate its growth. Typically, this occurs when the bacteria help a plant to acquire essential nutrients. In particular, these nutrients include nitrogen, phosphorus and iron. Nitrogen gas which makes up approximately 20% of the atmosphere is inert an cannot be used in that form. However, some bacteria can convert nitrogen gas into a usable form that is essential for many plant and bacterial molecules including proteins and nucleic acids (such as DNA and RNA). Similarly, plant growth-promoting bacteria may help plants to take up various forms of phosphorus from

the soil. When plant growth-promoting bacteria secrete weak organic acids (such as acetic acid) into the soil this helps to release phosphorus from inorganic complexes that it may have formed with soil particles and minerals. In addition, some plant growth-promoting bacteria produce and secrete certain enzymes that can break down organic forms of phosphorus which can then be taken up by the plant. Here again, the phosphorus is a key component of a plant's (and a bacterium's) metabolism, being used to synthesize many proteins and all nucleic acids. Although iron is abundant in most soils, it usually exists in a form where plants and bacteria cannot utilize it to any great extent. Fortunately, many plant growth-promoting bacteria synthesize and secrete certain small molecules that can bind very tightly to iron molecules before the plant takes up this complex and assimilates the iron.

The direct promotion of plant growth may also occur as a consequence of plant growth-promoting bacteria regulating the amount of certain plant hormones, molecules that regulate various aspects of a plant's growth and development. Thus, plant growth-promoting bacteria may synthesize one or more of the following plant hormones: auxins, cytokinins, or gibberellins. In the plant growth-promoting bacteria that have been studied until now, the majority (65-90%) synthesize auxins while only a few (1-10%) of these bacteria have been shown to synthesize cytokinins and/or gibberellins. In addition, many plant growth-promoting bacteria produce an enzyme that can lower the amount of the plant hormone ethylene that the plant produces. This enzyme is especially useful to plants during periods of environmental stress (e.g. flooding, drought, high levels of salt, etc.) since plants often respond to environmental stress by synthesizing high levels of ethylene which are inhibitory to plant growth.



The pathogens are depicted in red and are shown as inhibiting the functioning of either the roots or the shoots of plants. Direct mechanisms of growth promotion mostly act by interacting with the plant roots. Indirect mechanisms function by interacting with the pathogen.

Indirect promotion of plant growth occurs when plant growth-promoting bacteria decrease or prevent the damage to plants that might otherwise occur from the action of various pathogenic agents. Plant growth-promoting bacteria that indirectly promote plant growth are sometimes called biocontrol bacteria or biocontrol agents. One of the major indirect mechanisms used by plant growth-promoting bacteria is the synthesis of antibiotics and other pathogen inhibitory compounds. Limiting the concentration of ethylene in a plant can also lower the damage caused by a pathogen. And, sequestering much of the potentially available iron in the vicinity of the pathogen will slow or prevent pathogen growth, because they also need iron for growth. Plant growth-promoting bacteria may also sometimes synthesize enzymes that degrade pathogen cell walls, or they may out-compete pathogens for binding sites on portions of a plant. Finally, plant growth-promoting bacteria can sometimes induce the plant to activate its own genes that provide it with some defenses against various pathogens (this is called induced systemic resistance).

4. ***The future of plant growth-promoting bacteria in plant agriculture.*** In the past 20 years or so, scientists have developed a relatively detailed understanding of many of the mechanisms that plant growth-promoting bacteria use to facilitate plant growth. Notwithstanding the fact that there are several plant growth-promoting bacteria that are currently being employed commercially, success in the laboratory does not always easily

translate into success in the field. Some of the factors that need to be considered when commercializing a plant growth-promoting bacterial strain include the following:

a. It is essential that the bacterial strain is thoroughly characterized in terms of understanding what plant growth-promoting mechanisms it contains as well as understanding what mechanisms the strain uses to survive in the soil/plant environment.

b. The strain must be easy and relatively inexpensive to grow on a large scale.

c. The strain must be formulated so that it can readily be shipped comparatively long distances and stored for several months without losing any of its effectiveness.

d. If a company produces plant growth-promoting bacterial strains for sale and use in several different countries, it is essential that the regulatory agencies in those countries have similar and consistent rules for the release of those bacterial strains in the environment.

e. It is essential that the public as a whole and farmers in particular develop a relatively sophisticated understanding regarding the many potential benefits of plant growth-promoting bacteria. This is important because at the present time many individuals in society naively regard bacteria as being largely sources of disease.

f. In the long term, it will important to develop new and efficient methods of treating plants with bacteria rather than chemicals.

g. Initially, plant growth-promoting bacteria will likely be applied one strain at a time. However, since no bacterial strains can provide all of a plant's needs, it is necessary to establish conditions for adding groups of bacteria in a single application (i.e., a bacterial consortium) where the various strains provide different and complementary benefits to the treated plants.

h. In the short term (the next 5-10 years) essentially all of the commercialized plant growth-promoting bacteria will be naturally-occurring bacterial strains. However, in the future, it will be possible to genetically alter some of these strains to make them more effective. To do this will require a significant change in attitude and perspective from both the public at large and the governmental regulatory agencies, i.e. a new perspective which emphasizes that genetic manipulation per se does not present any risk or hazard to the food supply.

i. Most soils also contain beneficial plant growth-promoting fungi called mycorrhizae. These fungi interact with the roots of more than 90% of all plants and help them to obtain water and nutrients from the soil. Importantly, plant growth-promoting bacteria and mycorrhizae use different mechanisms to promote plant growth but they are able to work together to perform this task.

The increased use of plant growth-promoting bacteria instead of agricultural chemicals is a change that is already happening. However, it will be many years before these bacteria will become the mainstay of global plant agriculture. In this context, it is useful to keep in mind that the large-scale production of transgenic plants has only existed for a little over 25 years; its use continues to grow despite opposition to that technology in many countries.

Relevance for Sustainable Development Goals and Grand Challenges

The exploitation of plant growth-promoting bacteria relates to several SDGs (*microbial aspects in italics*), including

- **Goal 2. End hunger, achieve food security and improved nutrition and promote sustainable agriculture** (*end hunger and malnutrition, increase agricultural productivity)*. By using plant growth-promoting bacteria instead of chemicals, it is possible to help plants to grow in different environments without polluting those environments. In this case, many fewer people will be exposed to the potentially toxic chemicals used in agriculture and eventually the cost of providing food to people, especially in poorer countries, will be decreased.

- **Goal 12. Ensure sustainable consumption and production patterns** *(achieve sustainable production and use/consumption practices, reduce waste production/pollutant release into the environment)*. Plant growth-promoting bacteria are naturally-occurring in all soils worldwide so they will not significantly alter the composition of local soils. They do not accumulate in the environment, nor do they produce any toxic compounds.

Potential Implications for Decisions

1. ***Individual***

a. Weighing up the various microbial and non-microbial factors and aligning them with personal convictions (what are the ways that we can continue to feed all of the people in the world without harming the environment?).

b. How would the use of plant growth-promoting bacteria instead of fertilizers and pesticides affect me as an individual)?

c. How do I explain to other people that the use of plant growth-promoting bacteria is a good solution to a problem that is not yet seen by many people as a problem?

2. ***Community policies***

a. Local environmental consequences (cleaner environment; long term solution to potential environmental problems)

b. *Non-microbial parameters: development of new agricultural companies; ability to support crops in the developing world.*

3. ***National policies relating to use of plant growth-promoting bacteria instead of agricultural chemicals***

a. Healthcare economics of allergies and related diseases, and positive influence on mental health

b. Environmental pollution

c. Ensuring safe drinking water supplies

d. Eutrophication/algal blooms/toxic algal blooms preventing use of surface water bodies, fisheries, tourism, etc.

e. Greenhouse gas production and global warming,

f. Sequestration of agricultural land otherwise used for food and renewable production.

Pupil Participation

1. Class discussion of the issues associated with plant growth-promoting bacteria

a. Why are bacteria commonly found in greater amounts around plant roots compared to the bulk soil?

b. What are some of the ways in which plant growth-promoting bacteria facilitate the growth and development of plants?

c. What are the differences between direct and indirect mechanisms of plant growth promotion?

d. What are some of the mechanisms that plant growth-promoting bacteria use to facilitate plant growth?

2. ***Pupil stakeholder awareness***

a. What are some of the advantages of using plant growth-promoting bacteria rather than agricultural chemicals?

b. What are some of the problems in commercializing the use of plant growth-promoting bacteria on a large scale?

c. Why might the general public be in favor (or against) the more widespread use of plant growth-promoting bacteria?

3. ***Exercises (could be made at any level, but these are probably secondary education level)***

a. In most places, the use of very large amounts of agricultural chemicals is not thought of as a problem. What other alternatives to agricultural chemicals can you envision?

b. Agricultural chemicals are produced in large commercial facilities, often exposing workers and people living nearby to high levels of these chemicals. Are there any risks associated with the large-scale growth of plant growth-promoting bacteria that could be used to replace those chemicals?

c. How can we change society's attitudes toward releasing large amounts of bacteria into the environment? How can we prove to people that plant growth-promoting bacteria are safe?

The Evidence Base, Further Reading and Teaching Aids

Ali, S. and Glick, B.R. 2019. Plant-bacterial interactions in management of plant growth under abiotic stresses. In: New and Future Developments in Microbial Biotechnology and Bioengineering. (Ed.) J.S. Singh, Elsevier. pp. 21-45.

Backer, R., Rokem, J.S., Ilangumaran, G., Lamont, J., Praslickova, D., Ricci, E., Subramanian, S. and Smith, D. 2018. Plant growth-promoting rhizobacteria: context, mechanisms of action, and roadmap to commercialization of biostimulants for sustainable agriculture. Front Plant Sci 9:1473.

Duca, D., Lorv, J., Patten, C.L., Rose, D. and Glick, B.R. 2014. Indole-3-acetic acid in plant-microbe interactions. Anton. Van Leeuwenhoek 106:85-125.

Forni, C., Duca, D. and Glick, B.R. 2017. Mechanisms of plant response to salt and drought stress and their alteration by rhizobacteria. Plant Soil 410:335-356

Gamalero, E. and Glick, B.R. 2019. Plant growth-promoting bacteria in agriculture and stressed environments. In: Modern Soil Microbiology, 3rd edition, Kluwer, (eds.) D. VanElsas and J.T. Trevors, pp. 361-380.

Gerland, P., Rafferty, A.E., Sevcikova, H., Li, N., Gu, D., Spoorenberg, T., Alkema, L., Fosdick, B.K., Chunn, J., Lalic, N., Bay, G., Buettner, T., Hweilig, G.K. and Wilmoth, J. 2014. World population and stabilization unlikely this century. Science 346:234-237.

Glick, B.R. 2012. Plant growth-promoting bacteria: mechanisms and applications, Scientifica vol. 2012, Article ID 963401. doi:10.6064/2012/963401.

Glick, B.R. 2020. Beneficial Plant-Bacterial Interactions, 2nd edition, Springer, Heidelberg, in press.

Kong, Z. and Glick, B.R. 2017. The role of bacteria in phytoremediation. In: "Applied Bioengineering: Innovations and Future Directions", Yoshida, T. (Ed.), Wiley-VCH Verlaf GmbH & Co., pp. 315-341.

Lugtenberg, B. (ed.) (2015) Principles of plant-microbe interactions. Springer, Heidelberg.

Reed, M.L.E. and Glick, B.R. 2013. Applications of plant growth-promoting bacteria for plant and soil systems. In: "Applications of Microbial Engineering". Gupta, V.K., Schmoll, M., Maki, M., Tuohy, M., and Mazutti, M.A. (eds.). pp. 181-229, Taylor and Francis, Enfield, Connecticut.

Rosier, A., Medeiros, F.H.V. and Bais, H.P. 2018. Defining plant growth promoting rhizobacteria molecular and biochemical networks in beneficial plant-microbe interactions. Plant Soil 428:35-55.

Sprent, J.I. 1986. Benefits of *Rhizobium* to agriculture. Trends Biotechnol 4:124-129.

Glossary

transgenic plants: plants that carry genes that were introduced by scientists