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To Rav Avram Hersh Glick,
Born circa 1850, died 1914
(Belz, Austria-Hungary)

And, to his great great great grandchildren
Benjamin, Aviva and Gabrielle Glick
Born 2009, 2011 and 2014, respectively
(Ottawa, Canada)

Preface

In recent years there has been considerable interest in studies involving plant growth-promoting bacteria (PGPB) and their interaction with plants. This interest is derived from the notion (hope) that these bacteria will eventually be used on a large scale in sustainable agricultural practice. In addition, the successful implementation of PGPB may enable them to partially, or even completely, replace the current excessive use of chemicals in agriculture. In fact, given the ever-increasing understanding of many of the fundamental biochemical and genetic mechanisms that are operative in plant–bacterial interactions, there is every reason to expect that we are on the verge of a new paradigm in agriculture where we are able to utilize this technology worldwide on a practical and large scale. Of course, for PGPB technology to continue to develop to realize its full potential, it is imperative that the fundamental research in this field continues unabated.

In the last 5–10 years, there have been a relatively large number of books dealing with various aspects of the interaction between plants and microorganisms. Nearly all of these books have been written by groups of specialists in this field and are intended for burgeoning practitioners. On the other hand, this book was written to serve as a textbook (guidebook) for a one-semester undergraduate or graduate course in Plant–Microbe Interactions. It is based on a course that has been offered at the University of Waterloo for the past number of years and attempts to present a broad, although admittedly biased, perspective of this area. The book assumes some basic knowledge of Microbiology, Plant Biology, Molecular Biology and Biochemistry. This notwithstanding, not everyone who uses this book will have had an extensive background in all of the above-mentioned disciplines. Therefore, this book is intentionally written in a jargon-free style in which as much

of the background as is necessary to understand the major concepts is provided. The book should therefore be useful to anyone who is interested in developing a relatively broad fundamental perspective on plant–microbe interactions.

Waterloo, ON, Canada Bernard R. Glick

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Chapter 1
Introduction to Plant Growth-promoting Bacteria

1.1 The Problem

The Reverend Thomas Robert Malthus (1766–1834) was a British cleric and scholar who became widely known for his theories about changes in the world's population. He promulgated the idea that "The power of population is indefinitely greater than the power in the earth to produce subsistence for man." That is, Malthus understood that sooner or later, the earth, which is finite, would be unable to produce enough food to feed all of the people who live here. Malthus' thinking was in direct opposition to the view that was popular in eighteenth-century Europe that society would continue to improve and was in principle "perfectible." Of course, neither Malthus nor any of his critics could have possibly predicted the enormous technological changes, including changes to agricultural and food storage technologies, that have taken place over the past 150–200 years. These changes have enabled the world's population to expand dramatically in a relatively short period of time. However, these technological changes may have lulled us into a sense of false security whereby many people in society, especially in more developed countries, believe that we have never had it so good, and as long as our policies continue to support innovation and business expansion, the good life will continue on well into the future. Unfortunately, at this juncture, the threat of insufficient food to feed all of the world's people is once again in the headlines. This is a result of a continuously growing world's population, worldwide climate change, food spoilage and wastage on an enormous scale, the unequal distribution of food resources around the world, and the over use of energy-intensive agricultural chemicals (Fig. 1.1).

At the present time, there are around 7 billion people in the world (Fig. 1.2), up from approximately 2.5 billion in 1950 and around 1 billion in the early 1800s, and is predicted to rise to somewhere around 9.5 billion by 2050. That is, the increase in the world's population in the next 35 or so years will be approximately equal to the number of people in the world in 1950. Put another way, within a

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Fig. 1.1 Schematic representation of some of the limitations on the ability of the world being able to feed all of the people

period of just 100 years (1950–2050), the world's population will increase nearly fourfold. Moreover, the rate of global industrialization continues to increase as does our use of and need for non-renewable resources. Thus, we are increasingly polluting the air, water, and soil all over the planet so that some 40 % of deaths worldwide have been estimated to be a consequence of that pollution. This is because, as a result of both increasing population and industrialization, the earth's atmospheric, terrestrial, and aquatic systems are no longer able to break down and tolerate the increasing amount of waste that human society produces. In fact, according to the United Nations Intergovernmental Panel on Climate Change

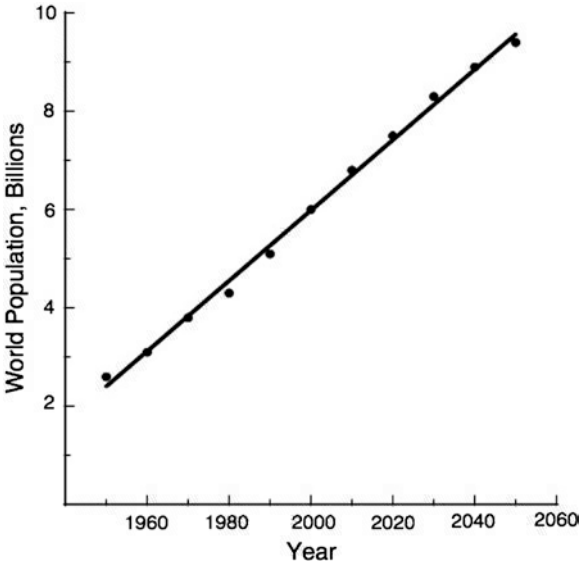

Fig. 1.2 Estimated world's population from 1950 to 2050

Report released in early 2014, the overall effect of various aspects of man-made global warming is that worldwide food production will be significantly reduced compared to a world without global warming.

Ironically, between 1960 and 2010, the fraction of the human population with insufficient food declined from about 60 % to around 15 % indicating that up until now food production has more than kept pace with population growth. However, put simply, the problem is whether we will be able to feed another 2+ billion people by 2050.

1.2 Possible Solutions

Given the issues that have been outlined above, it is imperative that worldwide action be taken on a variety of fronts. This includes the need to dramatically increase agricultural productivity within the next few decades. To do this, in the first instance, it is necessary to limit increases to the world's population, an extremely controversial subject at best. Next, it is necessary to be able to more efficiently deliver food from where it is produced to where it is consumed thereby decreasing much of the food spoilage that is common at present. Decreasing food wastage also entails addressing issues such as portion size in restaurants in more affluent countries. Then, efficient and productive agriculture needs to be practiced on what is now considered to be marginal land. To boost crop yields, in the short term, it will be tempting to use even more agricultural chemicals than at present. However, such an approach will certainly be counterproductive in the longer term. Thus, instead of the increased use of chemicals, it is essential that the use of transgenic plants and the

widespread application of plant growth-promoting microorganisms, both bacteria and fungi, be embraced and practiced on a large scale.

Given the enormous amount of experience that scientists have had with transgenic plants over the past 35 or so years, it is the time for informed scientists to take the lead and educate both the public and the politicians regarding the many potential benefits of this technology. And where there are perceived problems with the development or use of transgenic plants, it is absolutely essential that sufficient resources of both time and money be directed to solving those problems for everyone's benefit. Transgenic plants have been produced in the field for human use since 1996, with 1.7 million farmers in 29 countries planting over 170 million ha of transgenic crops in 2012. In addition, the amount of land devoted to the growth of transgenic plants continues to grow (doubling every 5–7 years). According to Dr. Florence Wambugu (Nairobi, Kenya), "The African continent urgently needs agricultural biotechnology, including transgenic crops, in order to improve food production. Famine provides critics with an opportunity to promote an anti-biotech message that only results in millions of people, who urgently need food, starving to death." Finally, transgenic plants are useful for a very wide range of applications besides increasing crop yields. These include developing plants with abiotic stress resistance, insect resistance, virus resistance, herbicide resistance, pathogen resistance, better controlled fruit ripening, increased nutritional content, altered flower color, and increased flower lifetime, as well as using plants to produce edible vaccines and a host of potentially less expensive human therapeutic agents.

The interaction between bacteria and plants may be beneficial, harmful, or neutral for the plant, and sometimes, the effect of a particular bacterium may vary as the soil conditions change (Fig. 1.3). Plant beneficial bacteria are often termed plant growth-promoting bacteria (PGPB). Bacteria that interact with plants but

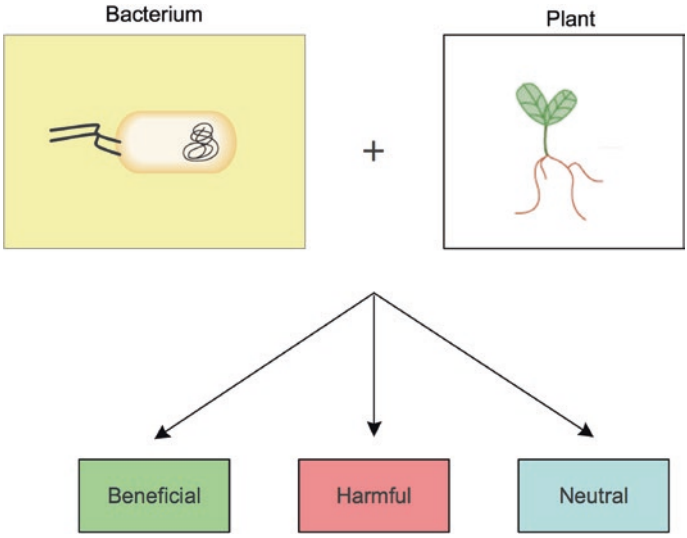

Fig. 1.3 Schematic representation of the possible effects of bacteria on plants

have no discernable effect on the plant (although there is often a benefit to the bacteria) are termed commensal bacteria. Bacteria that are harmful to plants are generally considered to be plant pathogens (phytopathogens). PGPB are typically defined as soil bacteria that facilitate plant growth and are often found in association with plant roots and sometimes found on plant leaves or flowers or within plant tissues. Given that some PGPB began to develop a complex and mutually beneficial relationship with flowering plants around 80–100 million years ago, the rationale behind the use of PGPB in agriculture is that this approach copies what has been successful in nature by deliberately adding PGPB to plants to facilitate their growth.

1.3 Plant Growth-promoting Bacteria

A large number of PGPB are commonly found in the plant rhizoplane, i.e., attached to roots, and the plant rhizosphere, i.e., the area immediately around the roots, generally up to 1 mm from the root surface (Fig. 1.4). This bacterial localization reflects the fact that plant roots commonly exude a significant fraction of the carbon that is fixed by photosynthesis (see below) and provide this fixed carbon to soil microbes that use it as a food source. Alternatively, some PGPB are endophytic (endo = inside; phyte = plant) and as such are able to enter into a

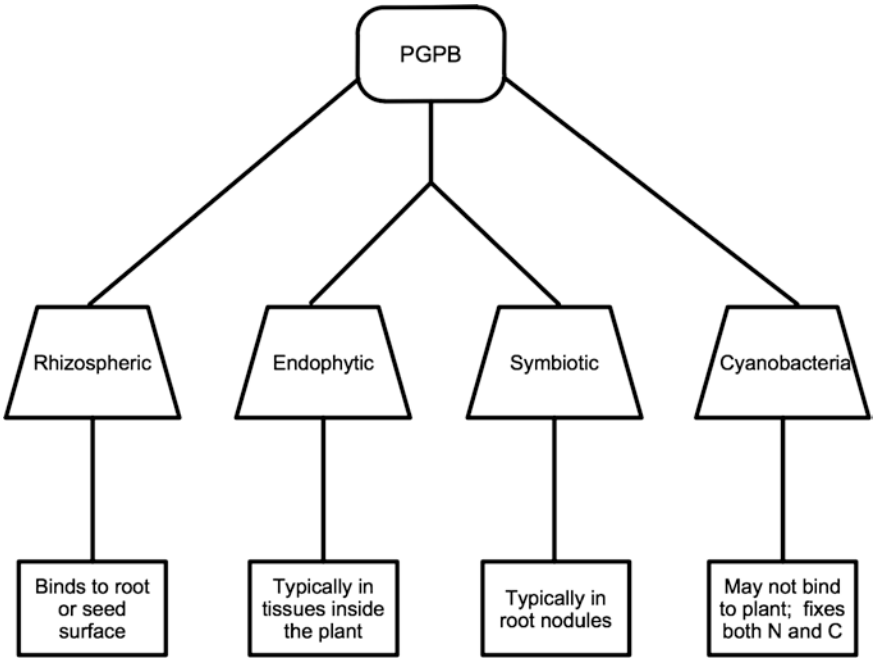

Fig. 1.4 Overview of different types of plant growth-promoting bacteria

plant and colonize a portion of the plant's interior. These bacteria do this without harming the plant and in fact use more or less the same mechanisms as rhizospheric bacteria to promote plant growth and development. Endophytic PGPB may be divided into two general types. First, those bacteria bind relatively nonspecifically to plant root surfaces and then enter the plant through different points including tissue wounds, stomata (pores found in the epidermis of leaves), lenticels (raised pores in the stems of woody plants), root cracks, and germinating radicals (the part of the embryo that develops into the root system). Second, those bacteria bind and infect only a very limited number of specific plants; these were formerly referred to as symbiotic bacteria (e.g., rhizobia that interact with specific legumes). Following infection, symbiotic bacteria typically form nodules on the plant root where this PGPB resides. Finally, although they are often not considered to be PGPB, many cyanobacteria are able to facilitate the growth of plants, usually aquatic plants. These cyanobacteria often fix both carbon and nitrogen; they sometimes but not always bind to plant surfaces.

1.3.1 Organisms in Soil

The natural world contains a very large number of species of different organisms, most of which are unknown and uncharacterized. For example, it has been estimated that there are nearly 8 million species of animals, ~300 thousand species of plants, 30–40 thousand species of protozoa, and 25–30 species of chromista (e.g., brown algae and diatoms). Being much smaller in size, the number of different microorganisms is very difficult to estimate so that recent estimates of the number of fungal species range from a mere 600 thousand to more than 5 million. Moreover, estimates of the total number of bacterial species in existence range from around 10 million to up to one billion. Given this perspective, it is not particularly surprising that the soil is home to a very large proportion of the world's biodiversity.

It has been estimated that there are more than 94 million organisms in a single gram of soil, with most of them being bacteria (Fig. 1.5). Of course, there really is no such thing as a typical gram of soil, and soils and their contents vary enormously from one location to another. Nevertheless, nearly all soils contain a surprisingly large number of microorganisms, the vast majority of which are bacteria. The main groups of PGPB can be found along with the phyla Cyanobacteria,

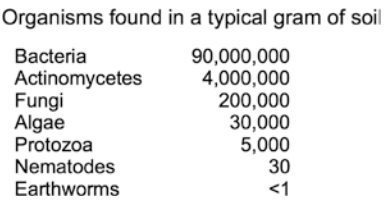

Fig. 1.5 Overview of the living organisms found in a typical gram of soil

Actinobacteria, Bacteroidetes, Firmicutes, and Proteobacteria. In addition to the very large number of bacteria that are typically found in soil, it has been estimated that many soils contain an equal or even greater number of viruses, largely bacterial and plant viruses. Unfortunately, it is extremely difficult to accurately estimate either the number or the types of viruses found in various soils. Given the fact that soil is an enormously complex environment, it is no surprise that plant growth and development is dramatically impacted by soil organisms, minerals, nutrients, and physical properties as well as a wide range of chemicals.

1.3.2 Root Exudation

The concentration of microbes around the roots of plants is typically 10- to 1,000-fold greater than the concentration of microbes found in the rest of the soil, which is sometimes called the bulk soil (Fig. 1.6). This is generally attributed to the fact that plants commonly exude from ~5 to ~30 % of all photosynthetically fixed carbon through their roots. Both the quantity and the composition of root exudates are determined by a number of different factors including plant species, plant age, plant cultivar (a variety of a plant that has been created or selected intentionally and maintained through cultivation), and the presence of biotic and abiotic environmental stressors. Although root exudation represents a significant cost to plants in terms of energy and carbon resources, root exudates have been suggested to play important roles in the functioning of plants. These roles include regulation of the local soil microbial community by secreting both chemical attractants and repellants, helping to cope with herbivores, changing the chemical and physical properties of the soil, and preventing the growth of potentially crop-inhibiting plant species. Root exudates are generally composed of low molecular weight compounds such as amino acids, sugars, organic acids, and phenolics as well as higher molecular weight compounds such as mucilage (viscous polysaccharides present in plant roots) and proteins. Sugars typically attract various microbes; flavonoids interact with mycorrhizae (a type of plant growth-promoting fungi),

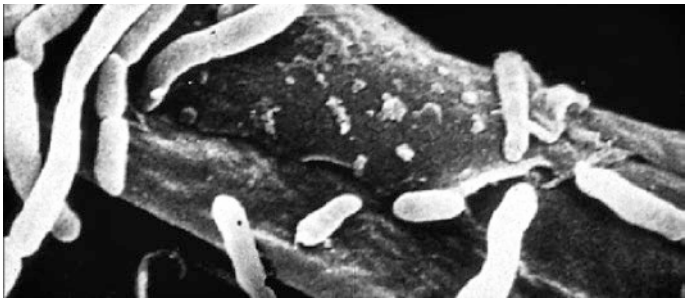

Fig. 1.6 Scanning electron micrograph of PGPB bound to a canola root hair

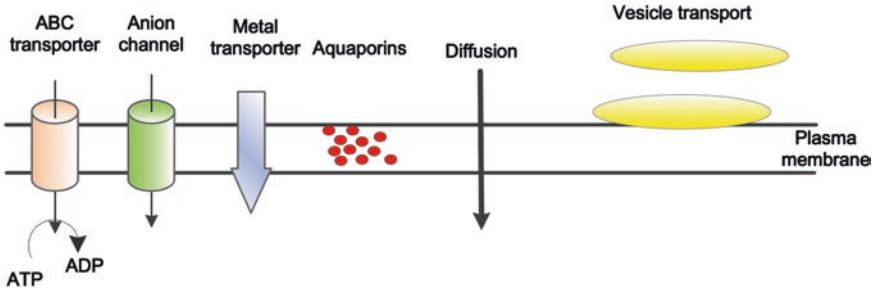

Fig. 1.7 Overview of the mechanisms which plant roots use to exude various compounds

rhizobia (bacteria that form a symbiotic relationship with specific legume plants), and pathogenic fungi; aliphatic acids attract certain bacteria; and fatty acids and proteins are also secreted.

The mechanism(s) by which plant roots secrete/exude compounds is considered to be a largely passive process. This can occur through diffusion, ion channels, or vesicle transport (Fig. 1.7). It is thought that ABC transporters, driven by ATP hydrolysis, are responsible for the exudation of lipids and flavonoids; anion channels for sugars and other carbohydrates; metal transporters for various metals; aquaporins (proteins embedded in the cell membrane) for water and uncharged molecules; diffusion for a range of low molecular weight compounds; and vesicles for high molecular weight compounds such as proteins.

Sometimes, root exudates contain antibiotics that inhibit the growth of either bacteria or fungi, as well as numerous other bioactive compounds. For example, root exudates of the plant *Lithospermum erythrorhizon*, a Chinese herbal medicine, produce pigmented naphthoquinones that have biological activity against soilborne bacteria and fungi. Isolating and identifying some of these compounds is an important step in developing some of them for use in combatting either plant or animal diseases. One way to isolate and identify unique bioactive compounds includes growing plants and collecting root exudates (Fig. 1.8), bioassaying the root exudates for various activities, and then fractionating the root exudates until a pure compound is obtained.

1.3.3 Effect of PGPB on Plants

PGPB have been documented to positively affect plants in a number of different ways. Thus, as a consequence of treating plants with PGPB, any one or more of the following may be observed: (i) increased biomass (Fig. 1.9); (ii) increased nitrogen, phosphorus, or iron content; (iii) increased root and/or shoot length; (iv) enhanced seed germination; (v) increased disease resistance; (vi) increased tolerance to various environmental stresses; (vii) increased production of useful secondary metabolites

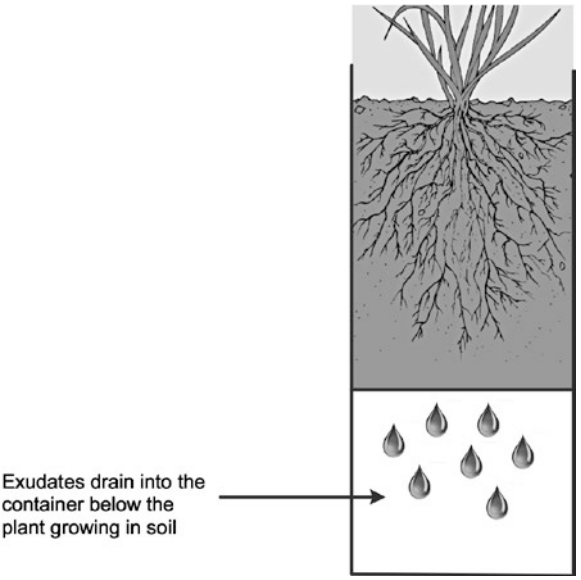

Fig. 1.8 A simple apparatus for collecting root exudates

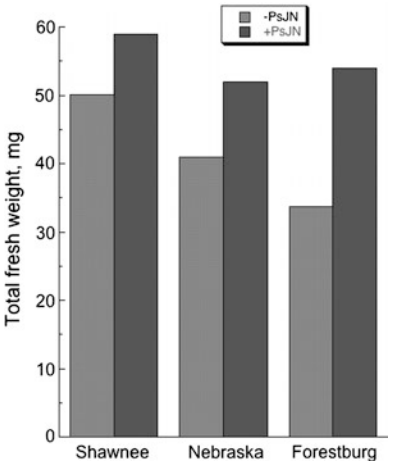

Fig. 1.9 Example of PGPB increasing plant biomass. Increase of switchgrass (*Panicum virgatum*) cv. Alamo biomass following one month of growth and treatment with the endophytic PGPB *Burkholderia phytofirmans* PsJN. Shawnee, Nebraska, and Forestburg are different cultivars of switchgrass. The data are from Biotechnol. Biofuels 5:37 (2012)

(e.g., essential oils in *Origanum majorana* or sweet marjoram (Fig. 1.10); and (viii) better plant nutrition, especially the edible portions of the plant.

In the example shown in Fig. 1.9, the well-characterized endophytic PGPB *Burkholderia phytofirmans* PsJN was found to significantly promote the growth (biomass production) of three different cultivars of switchgrass (*Panicum virgatum* cv. Alamo). Switchgrass is a non-crop plant that grows well on marginal land (generally considered to be unsuitable for agriculture) that may be useful as a so-called biomass crop, in this case used for the production of ethanol or butanol, or as a component of phytoremediation protocols (see Chap. 7).

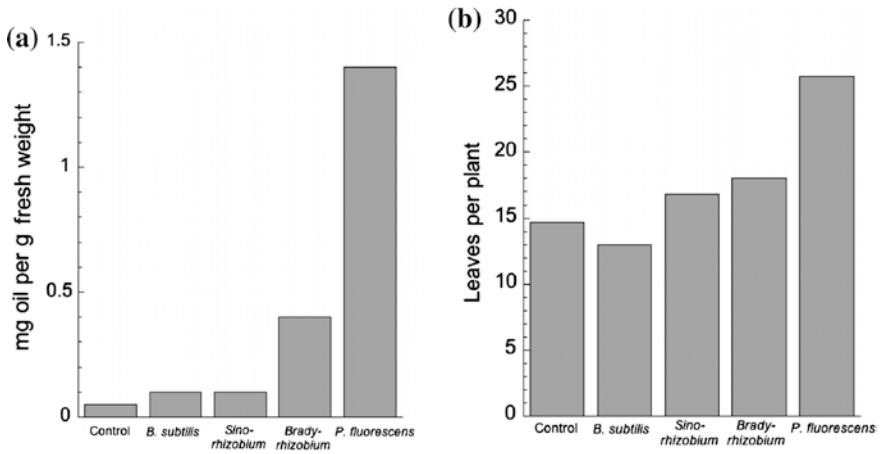

Fig. 1.10 Example of PGPB increasing plant oil production. Testing of four different putative PGPB for the ability to increase **a** essential oil production and **b** leaf number in *Origanum majorana* (sweet marjoram) plants treated with the indicated bacteria. The data are from Biochem. Systemat. Ecol. 36:766–771 (2008)

PGPB may stimulate plant growth in a variety of ways other than by merely increasing biomass. For example, several different PGPB strains (previously shown to increase plant biomass) were tested for the ability to promote the production of an essential oil in the plant *Origanum majorana* (sweet marjoram). In this case, the *P. fluorescens* strain was slightly better than the other PGPB that were tested in facilitating plant growth. However, the *Pseudomonas fluorescens* strain promoted the production of the essential oil (used to flavor foods and in fragrances) produced by this plant nearly 30 times compared to the untreated (control) plant (Fig. 1.10). Importantly, the composition of the essential oil remained unchanged following bacterial treatment of the plant roots. In addition, another PGPB strain, also a strain of *P. fluorescens*, was found to enhance both biomass yield and ajmalicine (an alkaloid that acts as an antihypertensive drug used in the treatment of high blood pressure) production in *Catharanthus roseus* (Madagascar periwinkle) plants that were subjected to water-deficit stress.

Another example of the effectiveness and possible practical use of PGPB comes from the observation that it is possible to select bacterial strains that, in addition to increasing plant biomass, can significantly increase the yield of chilli fruit (*Capsicum annuum* L.) under field conditions. In this work, scientists isolated a number of rhizosphere bacteria and then tested them for the ability to produce the plant hormone indoleacetic acid (IAA) and iron-binding siderophores; then, 15 selected strains were tested for the ability to promote plant growth in pots in the greenhouse. The three most effective strains were then tested in the field for the ability to increase the yield of chillies. As shown in Table 1.1, when two of the selected strains were applied together, the fruit number and biomass increased dramatically. In the end, with the best strain combination, it was possible to increase

Table 1.1 Effect of bacterial isolates on the yield of chilli (*Capsicum annuum* L.) under field conditions

Treatment	Plant height (cm)	Number of chilli fruits per plant	Biomass of chilli fruits per plant (g)
Growth medium	36.34	40.58	65
Strain C2	37.40	85.42	223.33
Strain C32	38.27	39.79	103.33
Strain C2 + strain C32	54.17	129.77	386.67

Strain C2 is a *Bacillus* sp.; strain C32 is a *Streptomyces* sp. The data are from Aust. J. Crop Sci. 4:531–536 (2011)

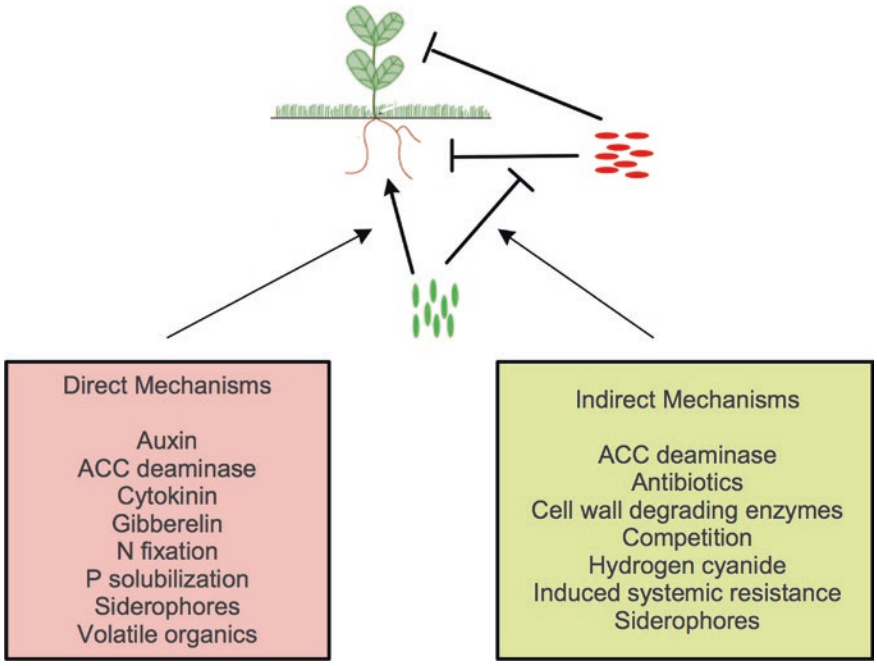

Fig. 1.11 Schematic representation of the main direct and indirect mechanisms used by PGPB to facilitate plant growth and development

the number of chillies per plant by approximately threefold and the biomass of chillies per plant by sixfold compared to the control that was untreated by added PGPB.

PGPB may affect plant growth and development either directly or indirectly (Fig. 1.11). Direct promotion of plant growth occurs when a bacterium either facilitates the acquisition of essential nutrient resources from the environment or modulates the level of hormones within a plant. Nutrient acquisition facilitated by PGPB, or at least the best studied of the nutrients in this category, includes

nitrogen, phosphorus, and iron. PGPB are known to directly affect plant growth by synthesizing and providing one or more of the phytohormones auxin, cytokinin, and gibberellin. In addition, some PGPB can lower levels of the phytohormone ethylene by synthesizing an enzyme, 1-aminocyclopropane-1-carboxylate (ACC) deaminase, that cleaves the compound ACC, the immediate precursor of ethylene in all higher plants. Indirect promotion of plant growth occurs when PGPB (sometimes called a biocontrol PGPB or just a biocontrol bacterium) prevent, or at least decrease, the damage to that might otherwise ensue as a consequence of the infection of the plant with any one of the various phytopathogens. These phytopathogens typically include various soil fungi and bacteria. In addition, PGPB, by a range of different indirect mechanisms, may lessen the damage to plants from either insects or nematodes.

Throughout the detailed discussions of PGPB mechanisms that appear in subsequent chapters in this book, it is essential to keep several things in mind. (i) Not all PGPB utilize the same mechanisms. (ii) Any particular PGPB strain may use any one or more of the many mechanisms that are discussed. (iii) A PGPB strain may use both direct and indirect mechanisms. (iv) Not all strains of the same genus and species have the same PGPB activities. (v) Different plants (including different cultivars of the same plant) may respond differently to a particular PGPB strain, usually reflecting differences in plant physiology/biochemistry. (vi) The same plant may respond differently to a particular PGPB strain, usually reflecting differences in plant physiology/biochemistry that are often a function of plant age and growth conditions (including soil composition, growth temperature, the presence or absence of stressful compounds, and/or phytopathogens).

Since rhizobial strains, that usually form a highly specific relationship with their plant hosts, employ more or less the same set of mechanisms as other PGPB, they are sometimes able to bind to the roots of non-legume plants and subsequently stimulate plant growth. Thus, it was recently observed that *Rhizobium leguminosarum* strain PEPV16 was able to colonize the roots of lettuce and carrot plants (both non-legumes) and promote the growth of both plants as well as increasing the uptake of N and P in the edible parts of both plants.

In addition to promoting the growth of crop plants in a traditional agricultural setting, PGPB may be used to stimulate the rooting of some vegetatively propagated plants such as olive plants. In Southern Spain, the world's largest olive oil producing region, there is significant motivation for production to be free of any chemical input including herbicides and pesticides. In one set of experiments, researchers added various PGPB to cuttings of three different olive tree cultivars. Although the results were somewhat variable, depending on the cultivar and the mode of adding the PGPB, the *Pantoea* strain was the only bacterial strain that always produces a high rooting percentage (typically equivalent to or better than the addition of indolebutyric acid, an analog of IAA). As this bacterial strain was not the best IAA producer, its effectiveness is thought to reflect a combination of IAA production and ACC deaminase activity (Table 1.2). This result was in agreement with other work where PGPB that both produced IAA and contained ACC deaminase activity produced a large number of relatively long roots (which are

Table 1.2 PGPB properties of several PGPB and their ability to promote rooting of "Picual" olive tree cuttings

Bacterial strain	IAA production (mg/L)	Siderophore production	Phosphorus solubilization	ACC deaminase activity	% Rooted cuttings
Azospirillum	20	−	−	−	10
Pantoea	21	+	−	+	38
Chryseobacterium	7	−	−	−	7
*Chryseobacterium*2	13	++	−	−	30
Pseudomonas	45	+++	+	−	16
Water	n.a.	n.a.	n.a.	n.a.	4
IBA	n.a.	n.a.	n.a.	n.a.	40

Chryseobacterium and *Chryseobacterium*2 are two different strains of this bacterium. IBA is indolebutyric acid. In this experiment, water acts as a baseline or negative control and IBA acts as a positive control

more effective in helping the plant to become established) compared to IAA or indolebutyric acid that produced a large number of very short roots. In summary, these experiments suggest that PGPB with appropriate traits may become effective components of the organic production of olive trees used for producing olive oil.

1.4 Root Microbiome

There are an enormous numbers of bacteria in soil, sometimes including as many as 10^6 different taxa (taxonomic groups such as bacteria of different genera and species) in a typical gram of soil. Given the diversity of soil bacteria, a question that arises is whether there are particular features that facilitate the colonization of plant rhizospheres by certain bacteria and not by others. To address this question, two groups of scientists separately used the technique of next generation sequencing (see Chap. 4) to elaborate the DNA sequences of all of the 16S rRNA genes (a part of the 30S small sub-unit of prokaryotic ribosomes) in soil, rhizospheric and endophytic bacteria from different strains of the plant *Arabidopsis thaliana* (Fig. 1.12). *Arabidopsis thaliana* (thale cress) is a small flowering plant related to cabbage and canola that is commonly used a model organism in plant biology, in part as a consequence of its very small genome (compared to nearly all other plants) that facilitates genetic studies. The sequence of the 16S rRNA is highly conserved between different species of bacteria so that its DNA sequence is used as a means of classifying bacteria into a particular genus and species. These two groups of researchers took soil, rhizospheric, and endophytic samples from several different *Arabidopsis* strains, each grown in different soils. Both of these groups reported that the composition of the rhizospheric and the endophytes microbiomes were defined primarily by soil type. In addition, the researchers reported that *Arabidopsis* contains a typical "core" microbiome, ~60 % of which is "recruited"

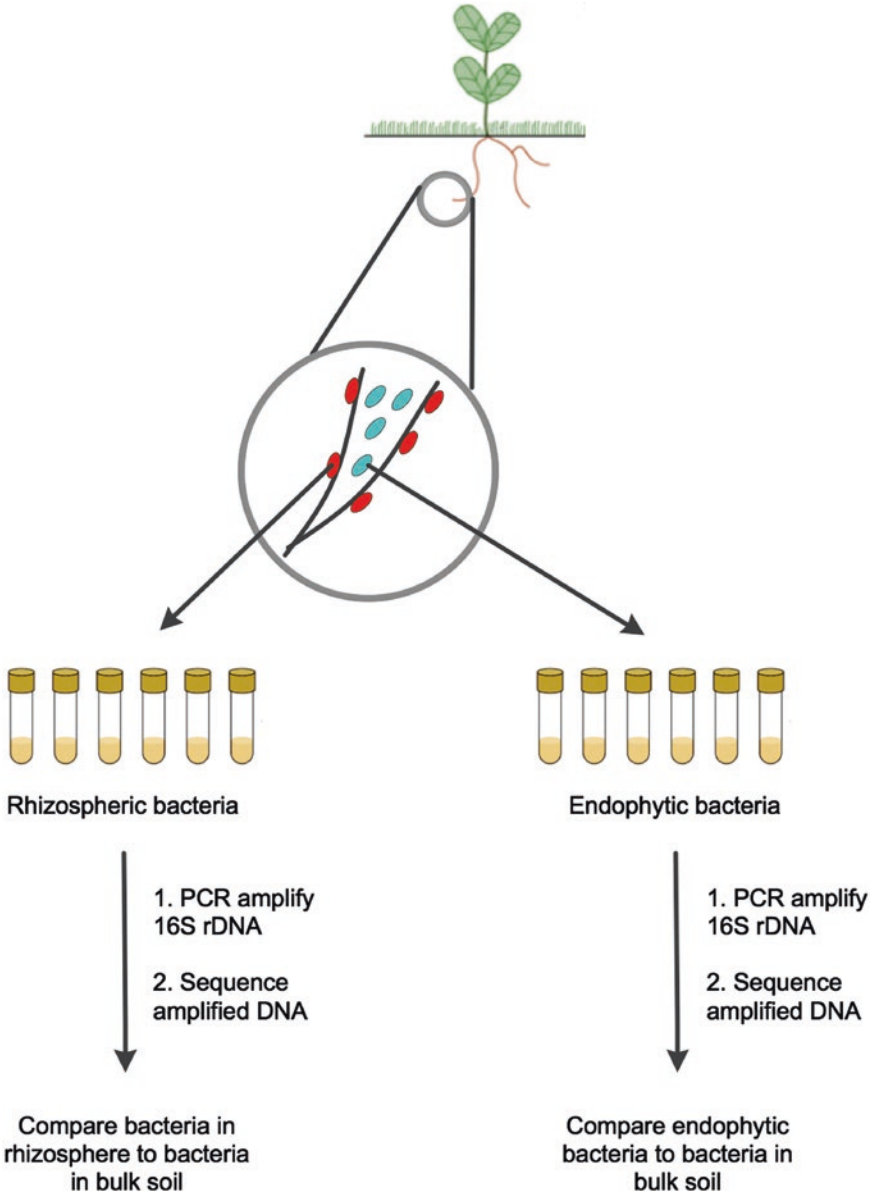

Fig. 1.12 Schematic representation of the identification of the bacteria that comprise the microbiome of *Arabidopsis*. *Red-colored shapes* represent rhizospheric bacteria bound to a root surface, while *blue-colored shapes* represent endophytic bacteria located within the root

from common soil bacteria. This core microbiome is "selected" by the ability of individual bacteria to grow in *Arabidopsis* root exudates. The remaining bacteria that were identified appeared to be responding and subsequently binding to

the plant root's lignocellulosic surface. These results were also independent of plant age. It remains to be demonstrated whether other plants behave similarly to *Arabidopsis* in selecting their microbiome from the soil; however, it is likely that this will turn out to be the case.

The root microbiome (rhizospheric and endophytic) may develop based on both positive and negative selection pressures that occur as a result of the composition of root exudates. For a start, soil bacteria are largely dependent upon exogenous carbon sources for both energy, and growth and development. The release of certain specific compounds by plant roots therefore select for the limited number of bacteria that are able to use those compounds. Moreover, root exudates are generally plant specific and the use of these specific compounds often acts as signals in establishing a plant's affinity for particular bacteria. For example, some rhizosphere bacteria can use indole acetic acid (IAA, auxin) produced by the plant as a carbon source for growth. Similarly, only a limited number of soil bacteria can utilize sulfur-containing compounds such as methionine for their growth. Those bacteria that can utilize the sulfur-containing compounds that are typically produced by cruciferous plants such as canola and cauliflower will therefore be found commonly in the microbiome of those plants.

1.5 PGPB Mechanisms

Historically, most of the interest in PGPB was based on the ability of either (i) some PGPB to act as biocontrol agents decreasing the damage to plants from phytopathogens or (ii) some rhizobia strains to form symbiotic relationships with specific legumes and then providing those plants with fixed nitrogen. In fact, these are still major interests of a large number of researchers in this field. As well, the vast majority of commercialized PGPB strains have been developed to address these two issues. This focus is most likely a reflection of the generally held view that in the field it is easier to reproducibly demonstrate the efficacy of biocontrol plant growth-promoting bacteria or nitrogen-fixing rhizobia rather than PGPB that promote plant growth in other ways.

As addressed briefly in Sect. 1.3.3, there are several ways in which different PGPB can directly facilitate the proliferation of their plant hosts (Fig. 1.11). PGPB may fix atmospheric nitrogen and supply it to plants; synthesize siderophores which can solubilize and sequester iron from the soil and provide it to plant cells; synthesize phytohormones such as auxins, cytokinins, or gibberellins which can enhance plant growth; provide mechanisms for the solubilization of phosphorus making it more readily available for plant growth; and synthesize the enzyme ACC deaminase which lowers potentially inhibitory plant ethylene levels. Any particular bacterium may affect plant growth and development using any one, or more, of these mechanisms. Moreover, a bacterium may utilize different traits at various times during the life cycle of the plant. For example, following seed germination, PGPB may lower the plant's ethylene concentration thereby decreasing the ethylene inhibition of