

Fertilizers

Components, Uses in Agriculture
and Environmental Impacts

Fernando López-Valdez
Fabían Fernández-Luqueño
Editors



Biotechnology in Agriculture, Industry and Medicine

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FERNANDO LÓPEZ-VALDEZ
AND
FABIÁN FERNÁNDEZ-LUQUEÑO
EDITORS

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This publication is designed to provide accurate and authoritative information with regard to the subject matter covered herein. It is sold with the clear understanding that the Publisher is not engaged in rendering legal or any other professional services. If legal or any other expert assistance is required, the services of a competent person should be sought. FROM A DECLARATION OF PARTICIPANTS JOINTLY ADOPTED BY A COMMITTEE OF THE AMERICAN BAR ASSOCIATION AND A COMMITTEE OF PUBLISHERS.

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PREFACE

The purpose of this book is to provide the state of the art of some important topics on subsistence agriculture, modern agronomy, and technological improvements which have sharply increased yields from cultivation, with special emphasis on the sustainable management and environmental impact of commercial and nontraditional fertilizers. We are really sure that this book provides cutting-edge knowledge in both theoretical and applied aspects of fertilizer management for undergraduate and postgraduate students, researchers, and other professionals in agricultural disciplines. This book is divided in five sections: **Section I** (*Traditional fertilizers*), where you can find two chapters about mineral fertilizers such as nitrogen and phosphorus, and their effects on the environment (atmospheric pollutants and dispersion in water bodies). The **Section II** (*Organic fertilizers*) presents two chapters about fishery wastes and biochar as an important alternative of fertilization and their effects on soil fertility and crop productivity. In the **Section III** (*Biofertilizers*), we provide two interesting chapters that compare the bio- and chemical fertilization with the biofertilizers as complements to chemical or organic fertilization. **Section IV** (*Non-conventional fertilizers*), where you can find interesting themes on silicon fertilizers, Nanofertilizers, and Non-traditional ameliorants, as others important sources of agricultural fertilizers. Finally, **Section V** (*Improving fertilizer applications*), we select this important topics as a complement for fertilizer application, that include topic as the modified natural rubber as controlling release of fertilizers, the effect of mulch materials on crop yield, and the radiological impact of fertilizers.

Certainly, this book is a valuable contribution to the agricultural sciences and it would not have been possible without the invaluable contribution, immeasurable acknowledge and recognized expertise from the authors.

The Editors

Chapter 6

BIOFERTILIZERS AS COMPLEMENTS TO SYNTHETIC AND ORGANIC FERTILIZATION

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ABSTRACT

Biofertilizers are agrobiotechnological products composed by microorganisms that are added to the agricultural crops to stimulate growth and production. Although they are sometimes considered as substitutes of the synthetic fertilizers, they indeed have been shown to act complementarily to chemical and organic fertilizers to improve plant performance. Synthetic fertilizers are added to the crops to support plant growth and foster crop production, but regrettably at most 50% of the synthetic nitrogen fertilizers can be absorbed by the plants. Microorganisms can positively affect plant performance in different ways, but they can also increase the percentage of the synthetic fertilizers that can be absorbed by the plants. In this chapter we will analyze the use of biofertilizers as complements to synthetic and organic fertilizers and the beneficial output of considering a chemical-organic-biological approach in crop production.

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INTRODUCTION

Biofertilizers, also known as bioinoculants, microbial inoculants or soil inoculants are agricultural biotechnology products that contain living or dormant microorganisms (bacteria or fungi, alone or in combination) that are added to agricultural crops to boost their growth and productivity.

The term “biofertilizer” derives from the words, biological and fertilizer, so that it refers to a biological fertilizer. In this context, a biofertilizer contains living microorganisms that have the capacity for improving the nutritional status of the plants. Conversely, organic products such as manure, crop residues, compost and vermicompost, which are also added to the crops to improve their nutrition, are not considered as biofertilizers but as *organic fertilizer*, although they indeed contain microorganisms, their identity and concentration normally remain unknown.

Due to the relative novelty of this technology in México and to the great impulse the government has settled for promoting the use of the biofertilizers in the Mexican agriculture many companies try their products be considered as biofertilizers, despite they do not meet the basic requirement of having axenically grown microorganisms. Also, in the worst cases these products can contain pathogenic microorganisms not only for plants but also for animals and the human being itself.

Currently, there are good perspectives for using biofertilizers as a mean to reduce pesticides and increase crop production, because the ever rising prices of the chemical fertilizers and cumulating evidence for environmental degradation caused by the use of agrochemicals is leading agricultural producers to look for cheaper and safer production practices not only for organic but also for conventional agriculture. Within these strategies, it is very important to consider an integrated plant nutrition system based on the use of low doses of chemical fertilizers, application of organic fertilizers (compost, vermicompost) and inoculation of microorganisms possessing capacities for improving the assimilation of the nutrients contained in chemical and organic fertilizers. In this chapter we will review the benefits and mechanisms by which the microorganisms can improve the nutrient and health status of the plants and show the advantages of considering an integrated plant nutrition system for crop production.

CLASSIFICATION OF BIOFERTILIZERS

The microorganisms possess a wide diversity of mechanisms by which they promote plant growth. Based on these mechanisms we recognize four major groups of plant growth promoting microorganisms:

a) *Microorganisms that incorporate nitrogen into the plant-soil system through biological nitrogen fixation*

The most efficient nitrogen fixers are bacteria belonging to the genera *Rhizobium*, *Ensifer* (formerly *Sinorhizobium*), *Mesorhizobium*, *Bradyrhizobium*, *Azorhizobium* and *Allorhizobium* (Bloemberg & Lugtenberg, 2001).

b) *Microorganisms that increase nutrient and water uptake*

This category includes the fungi which associate with plants to form the symbiotic relationship known as mycorrhizae, which play an important role in water, phosphorus, zinc, sulfur, and copper uptake (Nelson & Spaner, 2010), and bacteria such as *Azospirillum* spp., which increases the capacity of water and nutrient uptake of plants by stimulating root growth through hormonal action. (Hayat et al., 2010).

c) *Microorganisms that increase the availability of nutrients found in the soil in not assimilable forms*

This category includes phosphate-solubilizing microorganisms capable of producing phosphatases or organic acids (e.g. *Bacillus megaterium* or *Pseudomonas fluorescens*), sulfur-oxidizing bacteria that convert elemental sulfur or any reduced form of this element into sulfates, which are the usable form by plants, microorganisms producing siderophores, such as certain species of the genera *Pseudomonas*, *Bacillus* and *Flavobacterium* that increase the availability of iron to the plants and microorganisms capable of destroy the structures potassium-bearing mineral (e.g. *Bacillus*, *Pseudomonas*, and *Clostridium* and fungi such as *Aspergillus*, *Penicillium* and *Mucor*; Guevara-Granja, 2010)

d) *Microorganisms that possess antagonistic activities against plant pathogens*

This mechanism is sustained by the fact that a healthy plant will feed and function better and, consequently, will be able to tolerate more efficiently the effect of nutritional deficiencies or adverse environmental conditions. Different species of *Pseudomonas*, *Bacillus*, *Serratia*, *Flavomonas*, *Curtobacterium* and *Trichoderma*, are included in this group (Aguado-Santacruz, 2012).

Additionally to the previous classification, other categories have been proposed for referencing the mechanisms by which the microorganisms promote the growth of plants:

a) *Biopesticides*

Include microorganisms that stimulate plant growth by controlling phytopathogenic agents. For example, *Pseudomonas aurantiaca* is an orange colored, Gram negative, growth-promoting bacterium originally isolated from the rhizosphere of potato that produces the compound di-2, 4 diacetylphloroglucylmethane, which is an effective antibiotic against various phytopathogenic soil microorganisms (Esipov et al., 1975; Felker et al., 2005). Additionally, some endophytic microorganisms such as *Cladosporium sphaerospermum*, *Neotyphodium* sp., *Phomopsis oblonga*, *Bacillus subtilis* or *Pseudomonas fluorescens* have

biocontrol activities against insects (Azevedo et al., 2000) and nematodes (Hallmann et al., 1997; Ryan et al., 2009) that are harmful to plants.

b) Phytostimulators or Biostimulators

This category includes microorganisms that promote plant growth usually by hormonal action. It has been elucidated that the main mechanism of the growth promoting bacterium *Azospirillum brasilense* is related to its ability to stimulate root growth through the production of indole acetic acid (IAA; Mascarua-Esparza et al., 1988). In addition to its effective capacity for fixing nitrogen, *Gluconacetobacter diazotrophicus* can produce IAA (Fuentes-Ramírez et al., 1993; Bastian et al., 1998) and cytokinins (Jiménez-Salgado et al., 1994), which could magnify the growth promoting activity of this bacterium. Likewise, some species of the genera *Pseudomonas*, *Azotobacter* and *Bacillus* release indole acetic acid, gibberellins and cytokinins into the rhizosphere of plants, exerting a growth stimulation which is specially marked at the seedling stage of plants (Lugtenberg & Kamilova, 2009).

Vessey (2003) considers that although biopesticides can stimulate plant growth by controlling pathogenic organisms, they do not have a direct effect on the nutritional status of plants and, therefore, should not be considered as biofertilizers. Based on this premise, some authors propose to differentiate the plant growth promoting bacteria (PGPB) into biocontrol-PGPB's and PGPB's depending on whether or not exhibit antagonism against pathogenic organisms (Bashan & Holguin, 1997).

Vessey (2003) also mentions that biofertilizers should include any microorganism that promotes plant growth by increasing the supply of primary nutrient availability to the host plant, either by promoting the resupplying of soil nutrients (*e.g.* through biological nitrogen fixation), increasing the availability of nutrients (*e.g.* solubilization of phosphates) or extending the physical access of the plants to these nutrients (*e.g.* increasing the volume or changing root architecture).

Under this definition, biofertilizers should include microorganisms incorporating new nutrients into the plant-soil system as well as microorganisms increasing the uptake and availability of nutrients. However, this raises a problem because many organisms have more than one mechanism to promote growth and can exhibit complementary biocontrol activities (Raupauch & Kloepper, 2000; Manjula & Podile, 2001; Guo et al., 2004). Based on these premises, some authors propose to use the term in a broader sense to include any biological product (or microorganism) capable of promoting plant growth regardless the mechanism used for this purpose; this is the meaning used for "biofertilizer" in this chapter of the book.

The benefits of using biofertilizers in agriculture include:

- Increased capacity of plants to absorb water and nutrients from the soil.
- Reduced demand of irrigation and fertilization doses in crops.
- Increased growth and seedling establishment.
- Increased rooting of cuttings.
- Increased vigor of seedlings and adult plants.
- Biocontrol of pathogens.
- Reduced time of harvest (in some cases between 7 and 9 days) and extension of the productive time of crops (Dibut & Martínez, 2004).

- Increased crop yields in both, field and greenhouse conditions.
- Increased weight and quality of fruits.
- Compatibility with organic production of agricultural crops.
- Reduction of environmental pollution through reduced use of pesticides and chemical fertilizers (Kennedy, 2001).
- Bioremediation of soils contaminated with petroleum derivatives and heavy metals. It is known that high concentrations of metals in the soil and plants affect crop growth and the symbiotic relationships, and consequently, crop yields by disruption of fundamental physiological processes, such as photosynthesis, respiration, protein synthesis and carbohydrate metabolism (Khan et al., 2009). Different experiments have demonstrated the great potential of plant growth promoting rhizobacteria (PGPR) and mycorrhiza for detoxification of organic pollutants (Lucy et al., 2004, Abdul, 2006). Sarabia-Ochoa et al. (2010) refer different examples of bioremediation by PGPR including lead and zinc (*Azotobacter chroococcum* HKN-5-1, *Bacillus megaterium* HKP1, *Bacillus mucilaginosus* HKK-1), nickel (*Bacillus subtilis* SJ-101), cadmium (*Brevundimonas* sp. KR013, *Pseudomonas fluorescens* CR3, *Pseudomonas* sp. KR017, *Rhizobium leguminosarum* bv. trifolii NZP561, *Mesorhizobium huakuii* subsp. regei B3), nickel, lead and zinc (*Khuyvera ascorbata* SUD165, *Khuyvera ascorbata* SUD165/26). In particular, the ability of *Burkholderia xenovorans* (formerly *Pseudomonas cepacia*, *Burkholderia cepacia* or *Burkholderia fungorum*) to degrade, chloroorganic pesticides and polychlorinated biphenyls (PCBs) is well documented. Kuiper et al. (2001) developed the concept of rhizoremediation, in which contaminant-degrading rhizobacteria, living on or close to the root, are selected for their ability to assimilate the root exudates rather than the chemical pollutants.

Certain microorganisms possess a wide range of added values. For example, some strains of *Pseudomonas* spp. have biocontrol activities against phytonematodes (Ali et al., 2002; Haas & Kell, 2003) and mollusks that represent a problem in water reservoirs (Molloy & Mayer, 2007). Some strains of *Pseudomonas cepacia* and *Pseudomonas solanacearum* are capable of hydrolyzing fusaric acid, which is the causative agent of wilt by *Fusarium* sp. (Sarabia-Ochoa et al., 2010).

Tsukamurella paurometabola C-924 is a tricalcium phosphate-solubilizing bacterium with nematocidal activity and capacity for producing indole acetic acid, proteases and chitinases. This bacterial strain also possesses antagonistic activities against phytopathogenic fungi such as *Sarocladium oryzae*, *Alternaria longipes*, *Pestalotia debaryanum* and *Pythium palmarum*, and stimulates the growth of maize plants under greenhouse conditions (Marin et al., 2013).

Several strains of *Paenibacillus polymyxa* have demonstrated plant growth promotion through biological nitrogen fixation and phosphate solubilization, while being capable of producing hydrolytic enzymes including proteases, 3-glucanases, cellulases, xylanases, lipases, amylases and chitinases, and a wide variety of secondary metabolites including auxins, cytokinins, lytic enzymes, and antibacterial and antifungal compounds. Likewise, *P. polymyxa* causes structural changes in the root of plants and exerts control over different phytopathogenic fungi such as *Botrytis cinerea*, *Fusarium oxysporum*, *Pythium* spp.,

Phytophthora palmivora, *Pythium aphanidermatum*, *Micrococcus* spp., *Aspergillus versicolor* and *Phytophthora capsici*, and against different parasitic nematodes of plants, including the root-knot nematode *Meloidogyne incognita* (Benítez-Noyola, 2013).

On the other hand, certain species of the biocontrol fungus *Trichoderma* sp. are efficient producers of many extracellular enzymes used in the food and textile industry. In addition, they also have a great potential for the production of lignocellulosic biofuels due to their ability to degrade complex polysaccharides (Kovacs et al., 2009).

Finally, another advantage of using microorganisms as a means to control plant diseases is that, unlike what happens with chemical pesticides, biofertilizers are less prone to induce resistance because they possess multiple mechanisms to control the pathogens.

ACTION MECHANISMS OF BIOFERTILIZERS

The mechanisms explaining the developmental and productivity responses of plants to the inoculation with beneficial microorganisms can be direct or indirect.

DIRECT MECHANISMS

Through these mechanisms, biofertilizers improve plant growth favoring the nutrition of crops, either by increasing the availability and uptake of nutrients and water via hormonal action or by altering the structure and the absorptive surface of roots.

Biological Nitrogen Fixation

This activity involves the enzymatic reduction of atmospheric nitrogen (N_2) to ammonium (NH_4). In some plants this reductive process is performed in specialized structures (such as the root nodules of legumes) and is catalyzed by the enzymatic complex of the nitrogenase, which consists of two different proteins: dinitrogenase, the molybdenum-iron protein, and dinitrogenase reductase, the iron protein (Seefeldt et al., 2009; Moure et al., 2013).

Synthesis of Hormones

Hormones are natural compounds that in low concentrations are able to affect fundamental morphological and physiological processes of plants. The production of hormones (auxins, gibberellins and cytokinins) has been one of the preferred mechanisms used by different researchers to explain the direct stimulation of growth by microorganisms (Brown, 1974; Patten & Glick, 1996; García de Salamone et al., 2005). In bacteria, particularly Gram-negative, production of indole acetic acid (IAA) is one of the most widespread mechanisms of growth promotion. The precursor of this hormone, the amino acid tryptophan, is one of the compounds mostly abundant in root exudates (Kamilova et al., 2006)

and IAA can be found in up to 80% of the bacteria isolated from the rhizosphere of some plants (Loper & Schroth, 1986).

Synthesis of Vitamins

The production of certain vitamins contributes significantly to the growth promoting activity of certain microorganisms. For example, it has been shown that *Pseudomonas fluorescens* strain 267 produces water soluble vitamins of the B group, which stimulate the growth of red clover, *Trifolium pratense* (Marek-Kozaczuk & Skorupska, 2001). Also, some strains of *Azotobacter* and *Azospirillum* produce B vitamins that increase the rooting capacity of plants and affect soil microbial populations (Rodelas et al., 1993; Revillas et al., 2000).

Regulation of the Ethylene Levels

Ethylene is a plant hormone that can inhibit the development of the root and, therefore, limit the ability of plants to absorb nutrients and water from soil. In higher plants, the enzyme S-adenosyl-L-methionine (SAM) synthase catalyzes the conversion of methionine to SAM (Giovanelli et al., 1980). In response to various types of stress, including mechanical injury, water stress (drought and flooding), salinity, herbicides, among others, the enzyme ACC synthase catalyzes the conversion of SAM to 1-aminocyclopropane-1-carboxylic acid (ACC), which is the immediate precursor of ethylene. Subsequently, ACC oxidase enzyme catalyzes the conversion of ACC to ethylene, carbon dioxide and hydrogen cyanide (John, 1991). This increase in the levels of ethylene in the root causes a delay in root growth. Some microorganisms, e.g. different species of the genera *Pseudomonas* and *Bacillus*, possess an enzyme called ACC deaminase, which hydrolyzes 1-aminocyclopropane-1-carboxylic acid, the immediate precursor of ethylene, to form ammonia and α -ketobutyrate (Mayak et al., 1999; Shaharoon et al., 2006; Glick et al., 2007) and, thereby, prevent the formation of ethylene. Consequently, when the ACC deaminase activity increases, the levels of ethylene in the plant decreases and root development is visibly increased (Muhammad et al., 2007).

Siderophore Production

Siderophores are molecules (mainly non-ribosomal peptides) with a high affinity for iron that are produced by various microorganisms and grasses (Neilands, 1952; 1995) to increase the bioavailability of this element. At neutral pH, the iron availability in the soil is limited to plants due to the low solubility of the mineral phases (such as iron oxides) that associate to this element. Siderophores dissolve these mineral phases forming soluble complexes of iron can be then introduced into plant cells by active transport mechanisms. Under anoxic conditions (low oxygen), iron is usually found in the oxidation state of Fe^{+2} (ferrous ion) which is a soluble form. However, under oxic conditions (i.e. high concentrations of oxygen), iron is found as ferric ion (Fe^{+3}) that is capable of forming different insoluble minerals. To obtain the iron from these minerals, cells produce siderophores that binds to iron with high

affinity and transport it inside the cells. Siderophores produced by different bacteria and fungi include ferrichrome (*Ustilago sphaerogena*), mycobactin (*Mycobacterium* sp), enterobactin and bacillibactin (*Bacillus subtilis*), ferrioxamine B (*Streptomyces pilosus*), azotobactin (*Azotobacter vinelandii*), pseudobactin (*Pseudomonas* B10), ornibactin (*Burkholderia cepacia*) and coprogen, ferricrocin and palmitoylcoprogen (*Trichoderma* spp). Fluorescent pseudomonads produce a peptide siderophore with high affinity for iron called pyoverdín (Madigan & Martinko, 2005).

Phosphate Solubilization

Phosphorus (P) is, after nitrogen, the most important macronutrient for plant nutrition and a critical element in agricultural and natural ecosystems worldwide. Phosphorus is an essential component of key molecules for organisms, including RNA, DNA, AMP, ADP, ATP and phospholipids.

The productivity of arid regions is particularly low due to scarce and erratic precipitation, but also to the low availability of phosphorus in the soil. The soil phosphorus is readily converted into insoluble complexes such as hydrous oxides (oxides, hydroxides and oxyhydroxides) of iron and aluminum, amorphous and crystalline aluminum silicate and calcium carbonate (Sample et al., 1980).

Although arid soils contain a high concentration of phosphorus, *i.e.* 557-729 kg/ha, depending on soil use only 2.4 to 3.9% is found in available forms for plants. Generally, 15 to 20% (97 to 110 kg/ha) of the total phosphorus is present in organic forms such as phytin, lecithin, phospholipids and other compounds, while the remaining 77-82% is available in inorganic forms such as tricalcium phosphate, and a smaller quantity as iron and aluminum phosphates (Rao & Tarafdar, 2002). Insoluble forms of phosphorus include aluminum phosphates on acid soils, and calcium phosphates on alkaline soils. Fixing reactions in the soil cause that only a small portion (10 to 15%) of the phosphorus applied to the crops as chemical fertilizer or manure can be used by plants during the same year of its application.

Phosphorus deficiency causes a reduction of plant growth, alteration of the leaves to a bluish-green color and formation of acid tasting and small fruits. Strategies to address the low availability of phosphorus include the use of organic sources of this element (phosphoric rock or fish phosphate fertilizers) and the use of phosphate solubilizing bacteria (PSB), which increase the availability of this element for plants. PSB constitute a beneficial bacterial group capable of hydrolyzing both organic and inorganic phosphorus from insoluble sources (Goldstein et al., 2003). PSB secrete both organic acids and phosphatases to convert insoluble phosphates into soluble ions of monobasic (H_2PO_4^-) and dibasic (HPO_4^-) phosphate, through the process known as mineral phosphate solubilization.

It is generally accepted that the main mechanism of mineral phosphate solubilization is associated with the production of low molecular weight organic acids, which chelate the cations bound to the phosphate through its hydroxyl and carboxyl groups, favoring its conversion to a soluble form. In addition, some PSB produce phosphatases, such as phytase, which efficiently hydrolyze the organic forms of phosphate. PSB possess the ability to solubilize compounds such as tricalcium phosphate, dicalcium phosphate, hydroxyapatite and phosphoric rock; the gluconic acid and 2-ketogluconic are the compounds most commonly referred as phosphate solubilizers. Various enzymes, such as nonspecific phosphatases,

phytases and C-P lyases release phosphorus from soluble organic compounds in the soil. C-P lyases break the bonds C-P in organophosphates (Barea et al., 2005).

The ability of organic acids to increase the availability of P is not only related to acidification of the plant rhizosphere, but also to their ability to form stable complexes with the Al and Fe. Organic acids increase the availability of micronutrients in the soil (Fe, Zn and Mn) by decreasing the pH in the rhizosphere or by chelating these micronutrients.

Solubilization of soil phosphates leads to an increase in the availability of phosphorus and, consequently, to increased absorption of this element by the plants (Gyaneshwar et al., 2002). Likewise, the organic acids participate in the soil in phenomena such as microbial chemotaxis and metal detoxification.

Some of the acids with phosphate solubilizing capacity secreted by the PSB include oxalic, citric, butyric, malonic, lactic, succinic, malic, gluconic, acetic, glyconic, fumaric, adipic, indole acetic and 2-ketogluconic. On the other hand, bacteria that solubilize phosphates through the production of organic acids include the genera *Achromobacter*, *Aerobacter*, *Agrobacterium*, *Azotobacter*, *Azospirillum*, *Bacillus*, *Burkholderia*, *Enterobacter*, *Erwinia*, *Flavobacterium*, *Mesorhizobium*, *Micrococcus*, *Pantoea*, *Pseudomonas*, *Rahnella*, *Rhizobium*, *Streptosporangium* and *Yarrowia* (Paredes-Mendoza y Espinosa-Victoria, 2010).

Potassium Solubilization

Potassium deficiency, also known as potash deficiency, is a plant disorder that is most common on light, sandy soils, because potassium ions (K^+) are highly soluble and will easily leach from soils without colloids (Datnoff et al., 2007). Potassium deficiency is also common in chalky or peaty soils with low clay content and on heavy clays with a poor structure. The main role of potassium is to provide the appropriate ionic balance for metabolic processes occurring in the cytosol, and as such functions as a regulator of various processes including growth regulation (Leigh & Wyn Jones, 1984). Plants require potassium ions for protein synthesis and for the opening and closing of stomata. A deficiency of potassium ions can impair a plant's ability to maintain these processes. Potassium also functions in other physiological processes such as photosynthesis, protein synthesis, activation of some enzymes, phloem solute transport of photoassimilates into source organs, and maintenance of cation:anion balance in the cytosol and vacuole. Typical symptoms of potassium deficiency in plants include brown scorching and curling of leaf tips as well as chlorosis between leaf veins.

Potassium can be immobilized in the soil forming mineral structures such as feldspars or micas. Certain strains of *Bacillus*, *Pseudomonas* and *Clostridium*, and fungi such as *Aspergillus*, *Penicillium* and *Mucor*, solubilize potassium by releasing organic and inorganic acids that react with the potassium bearing-minerals. These microorganisms decompose aluminosilicates and release part of the potassium contained in them (Delgado-Higuera, 2002). Wuxing et al. (2007) demonstrated that *Bacillus mucilaginosus* is able to solubilize K^+ and SiO_2 silicates. This bacterium dissolved solid minerals and mica simultaneously, releasing K^+ and SiO_2 , but was unable to solubilize feldspar. *Frateruria aurentia* is a potassium-solubilizing bacteria widely used in the fabrication of biofertilizers that can act in any kind of soil, using carbon, sugars, organic acids and amino acids from the soil or root exudates (Guevara-Granja, 2010).

Sulfur Solubilization

Sulfur is the fourth most important element for plant growth after nitrogen, phosphorus and potassium. Sulfur importance is equal to that of the nitrogen in terms of protein synthesis, while in terms of assimilation by crops is greater than that of the phosphorus (Vidyalakshmi & Sridar, 2007). The original source of sulfur in the earth was igneous rocks, primarily igneous pyrite (FeS_2). Since then, the amount of sulfur in the environment has increased due to volcanic activity and weathering of the earth's crust in an oxygen atmosphere (Hoffman et al., 1998). Current sulfur sources come from the weathering of soil minerals, atmosphere and sulfur already fixed in the organism's biomass.

The essential processes of the sulfur cycle in nature are:

- 1) Mineralization of organic sulfur into inorganic forms, such as hydrogen sulfide (H_2S), elemental sulfur, as well as sulfide minerals.
- 2) Oxidation of hydrogen sulfide, sulfide, and elemental sulfur (S) to sulfate (SO_4^{2-}).
- 3) Reduction of sulfate to sulfide.
- 4) Incorporation of sulfide into organic compounds (including metal-containing derivatives).

Transfer of sulfur between organic and inorganic sources within the sulfur cycle is caused entirely by the activity of soil biota, particularly by the microbial biomass, which has the greatest potential for mineralization and the subsequent transformation of the oxidation state of sulfur.

Sulphate is the main form of sulfur assimilated by plants, so this element has to be first converted into this salt to be assimilated by plants (Mahendra, 1988). Sulfur oxidation leading to the formation of sulfate is the most important process in the sulfur cycle that leads to increased soil fertility. Additionally, soil acidification resulting from this oxidation process, help solubilizing nutrients and improve fertility in alkaline soils (Wainwright, 1984). The reduced inorganic sulfur compounds are oxidized exclusively by prokaryotes, although fungi such as *Alternaria tenuis*, *Aureobasidium pullulans*, *Epicoccum nigrum*, *Scolecobasidium constrictum*, *Myrothecium cinctum*, *Aspergillus* and a number of species of the genus *Penicillium* are capable of oxidizing elemental sulfur and thiosulfate (Vidyalakshmi et al., 2009). On the other hand, the oxidation of sulfur in members of the genus *Eukarya* is conducted by bacterial lithoautotrophic endosymbionts (Nelson & Fisher, 1995).

Prokaryotes have the ability to oxidize hydrogen sulfide, sulfur, sulfite, thiosulfate and different polythionates under alkaline, neutral or acidic conditions (Harrison, 1984; Sorokin et al., 2001). The sulfur-oxidizing aerobic prokaryotes belongs to genera *Acidiamus*, *Acidithiobacillus*, *Aquaspirillum*, *Aquifex*, *Bacillus*, *Beggiatoa*, *Methylobacterium*, *Paracoccus*, *Pseudomonas*, *Starkeya*, *Sulfolobus*, *Thermithiobacillus*, *Thiobacillus* and *Xanthobacter*, which are basically mesophilic microorganisms. Photoautotrophic, anaerobic, sulfur-oxidizing bacteria are primarily neutrophilic and mesophilic and belong to genera such as *Allochromatium* (formerly *Chromatium*), *Chlorobium*, *Rhodobacter*, *Rhodospseudomonas*, *Rhodovulum* and *Thiocapsa* (Friedrich et al., 2001).

Sulfur-oxidizing microorganisms are primarily Gram-negative bacteria of the genera *Thiobacillus*, *Thiomicrospira* and *Thiosphaera*, although some heterotrophic bacteria such as

Paracoccus, *Xanthobacter*, *Alcaligenes* and *Pseudomonas* may also exhibit chemolithoautotrophic growth on inorganic sulfur compounds (Vidyalakshmi et al., 2009).

Production of Volatile Compounds

Volatiles constitute a group of compounds that evaporate rapidly at ambient temperature and pressure. Some strains of rhizobacteria belonging to *Bacillus subtilis*, *Bacillus amyloliquefaciens* and *Enterobacter cloacae* promote plant growth releasing volatile compounds (Ryu et al., 2003). Growth promoting action by volatile compounds is one of the mechanisms more recently studied in PGPR. Acetoin (3-hydroxy-2-butanone) and 2,3-butanediol are volatile compounds produced by *B. subtilis* and *B. amyloliquefaciens*, which promote growth of *Arabidopsis thaliana* *in vitro*. Some of these compounds act by regulating the synthesis of auxin and cell expansion (Zhang et al., 2007), but a role has also been proposed in induction of systemic resistance (Farag et al., 2006) and antibiosis (Mitchell et al., 2010). Certainly, this knowledge area requires further research to identify new compounds and elucidate new plant signaling pathways involved in the interactions with plant growth promoting microorganisms. For example, two new volatile compounds, the 2-methyl propanoic acid and 3-methyl butanol, which are synthesized *de novo* during the interaction of *Arabidopsis thaliana* with the bacteria *Bacillus megaterium* and *Stenotrophomonas maltophilia* has been recently identified (Kai et al., 2007; García-Juárez et al., 2010).

Furthermore, in biocontrol fungi (*e.g.* *Trichoderma* spp.) certain volatile compounds, such as acetone, 2-methyl-1-butanol, heptanal and octanal, increase the antagonistic activity of the beneficial fungi by inhibiting the protein synthesis of pathogen fungi (Humphris et al., 2001). Additionally, *Arthrobacter agilis* UMCV2 is capable of producing volatile organic compounds (VOCs), primarily dimethylhexadecylamine, an amino lipid with antifungal activity, which exerts a strong inhibition on *Botrytis cinerea* and *Phytophthora cinnamomi*. Conveniently, the effect of this VOC on *Trichoderma virens* is very subtle, suggesting the possibility of developing comprehensive strategies for disease control considering this differential action (Velázquez-Becerra et al., 2010).

Synthesis of Pyrroloquinoline Quinone

Pyrroloquinoline quinone (PQQ) is a novel, water soluble and heat stable growth factor in plants that has the ability to carry our redox cycles (Stites et al., 2000). It has been reported that PQQ acts as a reactive oxygen species (ROS) scavenger by directly neutralizing reactive species in *Escherichia coli* (Misra et al., 2004). PQQ acts as a non-covalently bound redox cofactor of several bacterial dehydrogenases. Several gram-negative bacteria are capable of producing organic acids by direct oxidation of aldehydes, which then diffuse in surroundings and help in the acidification of poorly soluble mineral phosphates such as calcium phosphate (Goldstein, 1986; Sashidhar & Podile, 2010). Glucose dehydrogenase (GDH) requires PQQ as a redox cofactor for direct oxidation of glucose to gluconic acid, which then helps in acidic solubilization of insoluble phosphates in soil. There are plant growth-promoting bacteria that use GDH-PQQ holoenzyme for solubilization of both inorganic and /or organic phosphates in soil (Han et al., 2008).

The Gram-negative bacterium *Rahnella aquatilis* is ubiquitous and is characterized by its beneficial metabolism leading to mineral phosphate solubilization, antimicrobial activity, nitrogen fixation and plant disease suppression (Calvo et al., 2007). This bacterium produces PQQ and its mineral phosphate solubilizing capacity is contributed by mechanisms similar to other phosphate solubilizing microbes. Strain HX2R of *R. aquatilis* has been used as a biocontrol agent for grapevine crown gall caused by *Agrobacterium vitis*. PQQ mutants of this bacterium become ineffective in its biocontrol activity. Different reports suggest that the GDH-PQQ holoenzyme is involved in production of antimicrobial compounds in *P. fluorescens* (Schnider et al., 1995; de Werra et al., 2009) and *Enterobacter intermedium* 60-2G (Han et al., 2008). Particularly, *E. intermedium*, a phosphate-solubilizing bacterium, has the ability to induce systemic resistance in plants against the soft rot bacterial pathogen *Erwinia carotovora* and the fungus *Magnaporthe grisea*. Mutations in PQQ cause *E. intermedium* lose their biocontrol ability and its capacity for enhancing the systemic resistance of plants (Han et al., 2008).

INDIRECT MECHANISMS

The indirect promotion of plant growth occurs when biofertilizers prevent, reduce or eliminate one or more pathogenic organisms (Glick et al., 1999; Hernández & Charlloux, 2001) through the following mechanisms:

Competition for Space and Nutrients

To exert their beneficial effect on plant growth, microorganisms must be rhizosphere-competent, *i.e.*, should be capable of compete with other microorganisms present in the rhizosphere for nutrients secreted by the root and the physical space available inside or over the root. Only a small part of the root surface is covered by bacteria. Favorite sites for bacterial growth are the junctions between epidermal cells and origin points of the lateral roots. Once soil microorganisms colonize plant roots, they colonize space and consume nutrients that otherwise could be used by plant pathogens (Kloepper et al., 1988, O'Sullivan & O'Gara, 1992).

Siderophore Production

Siderophore synthesis is a dual mechanism for promoting plant growth, since it increases iron availability to plants but also contributes to biological control of phytopathogenic agents. Sequestering iron from the soil and making it available for themselves and for plant cells capable of assimilating the bacterial siderophore-iron complexes, plant growth promoting microorganisms can limit the pool of this element for other microorganisms that are unable to access the sequestered iron (Castignetti & Smarrelli, 1986; O'Sullivan & O'Gara, 1992; Dowling et al., 1996).

Antibiotic Synthesis

Production of antimicrobial compounds has been documented in several plant growth promoting microorganisms (O'Sullivan & O'Gara 1992; Haansuu et al., 1999) and this is the mechanism most commonly associated with the ability of biofertilizers to inhibit phytopathogens (Keel et al., 1992; Chet & Inbar, 1994; Whipps, 1997). The ability of some bacteria to suppress fungal pathogens depends on their ability to produce antibiotics such as pioluteorina, pirronitrina, fenacin-1-carboxylic acid and 2,4-diacetylphloroglucinol (Picard, et al., 2000). Other compounds with pathogen-inhibiting capacities released by bacteria include hydrogen cyanide (HCN) and/or lytic enzymes such as chitinase, β -1,3 glucanase, proteases and lipases (Friedlander et al., 1993; Chet & Inbar, 1994). Though pectinolytic activities are commonly associated with pathogenic bacteria, some species of non-pathogenic bacteria such as *Rhizobium* (Angle, 1986), *Azospirillum* (Umali-Garcia et al., 1980; Tien et al., 1981), *Klebsiella pneumoniae*, *Yersinia* (Chatterjee et al., 1978) and *Frankia* (Séguin & Lalonde, 1989) are also capable of degrading pectins. In general terms, pectinolytic enzymes play a role in the invasion of the roots by bacteria.

Induction of Systemic Resistance

Research on the benefits of microbial inoculants extends beyond their capacities to improve plant nutrition, since microbial inoculants can also trigger the mechanism of systemic acquired resistance (SAR) of plants to different phytopathogenic agents such as *Blumeria graminis*, *Gaeumannomyces graminis*, *Fusarium culmorum* and *Pseudomonas syringae* (Heitefuss, 2001; Waller et al., 2005; Khaosaad et al., 2007; Ramos-Solano et al., 2008). In plants, the SAR is a global resistance response that occurs after plants have contact with a pathogen or a product derived from it. In a broad sense, the systemic acquired resistance in plants is equivalent to the response of the immune system of animals to the attack by pathogens. After an early and localized exposure to certain infectious organisms, SAR activates the resistance mechanisms at the whole plant level against a wide variety of pathogens, (including to that initiating the response), so it is considered as a wide-spectrum response. It has been shown that endophytic colonization of cocoa seedlings by *Trichoderma* activates the plant defense signaling cascades (Bailey et al., 2006). SAR is associated with the induction of a great variety of genes (genes PR's or pathogenesis related) and requires the accumulation of endogenous salicylic acid.

SAR is associated with the ability to induce cellular defense responses more rapidly and to a greater degree than in non-induced plants, a process called "priming." The phenylalanine ammonia lyase (PAL) gene activation and callose deposition are among the main cellular defense responses induced by SAR.

Plant growth-promoting rhizobacteria can effectively induce pathogen resistance by triggering the expression of the hypersensitive response (HR) of plants, enhance lignification and callose deposition, increase hydrogen peroxide production and expression of the defense enzymes β -1,3-glucanase, chitinase, phenylalanine ammonia lyase, peroxidase and polyphenol oxidase (Niranjan-Raj et al., 2006).

Strain 63-28 of *Pseudomonas fluorescens* functions as an activator of disease resistance of plants by inducing the synthesis of callose in tomato (MPiga et al., 1997), while the application of saprophyte fluorescent pseudomonads in beans resulted in increased lignin content in the root (Anderson & Guerra, 1985).

Serratia plymuthica, strain R1GC4, sensitizes cucumber plants to react more quickly and effectively against the attack by *Pythium ultimum*, through the formation of physical and chemical barriers to impede the penetration of the fungi (Benhamou et al., 2000).

Formation of Biofilms to Prevent the Entry to Pathogens

Frequently, bacteria live in the environment as biofilms, which are highly structured, surface-attached communities of cells encased within a self-produced extracellular polymeric substance matrix (O'Toole et al., 1999; 2000; Branda et al., 2005; Kolter & Greenberg, 2006). Bacterial biofilms established on plant roots could protect the colonization sites and act as a sink for the nutrients in the rhizosphere, hence reducing the availability of root exudate nutritional elements for pathogen stimulation or subsequent colonization on the root (Weller & Thomashow, 1994). Particularly some strains of *Paenibacillus polymyxa* can form biofilms around the root tips of some plants to improve drought tolerance and to prevent the access to pathogens (Timmusk et al., 2005; Singh et al., 2006).

INTEGRATED PLANT NUTRITION SYSTEM (IPNS): COMBINED USE OF BIOFERTILIZERS AND CHEMICAL OR ORGANIC FERTILIZERS

One of the most important requirements in agriculture is the maintenance of soil fertility. Traditionally, nutrient deficiency, especially of N, is corrected by adding fertilizers. However, the high costs of these chemical products limit this practice, especially in developing countries, where the need to increase food production is more urgent (Aguado-Santacruz et al., 2012). It is estimated that crops absorb between 20-40% of the fertilizer applied because the rest is lost in different ways, generating substantial economic losses and environmental pollution such as eutrophication of water bodies, acid rain, destruction of the stratospheric ozone layer and increased greenhouse effect (Duxbury, 1994). On the other hand, some other sources, mainly organic fertilizers (compost, vermicompost and manures) and more importantly the Nitrogen Biological Fixation (NBF), can also contribute significantly to the N soil economy.

The IPNS basic concept is the adjustment of soil fertility for providing the optimal plant nutrients in order to maintain high crop productive levels taking advantage of the benefits from all of the possible sources of nutrients in an integrated manner (Jen-Hshuan, 2006). The implementation of sustainable technologies, such as biofertilization, to complement and enhance the assimilation of nutrients from chemical synthetic fertilizer and organic fertilizer, has been assessed in different studies that report satisfactory performance of different crops cultured under different environments emphasizing the necessity of considering complementary nutritional sources and tools for augmenting the nutrient assimilation by agricultural crops.

Different studies report a better assimilation of nutrients when the chemical fertilization is complemented with beneficial microorganisms. For example, Sundara et al. (2002) found that the application of the PSB *Bacillus megatherium* var. *phosphaticum* increase the availability of P in the soil, improving growth, yield and quality of sugarcane. When used in conjunction with phosphate fertilizers this PSB reduce the required dose of P by 25%. Moreover, it was shown that when applied in combination with phosphate rock, *B. megatherium* can help saving up to 50% of the production costs by replacing superphosphate. The effects of a combined treatment consisting of a multifunctional biofertilizer (mixture of *Bacillus* sp., *B. subtilis*, *B. erythropolis*, *B. pumilus* and *P. rubiacearum*) plus 50% of the recommended chemical fertilization dose was compared with the complete chemical fertilization dose on the growth of lettuce and water celery. The results of this study indicated a 25% increase of lettuce yield and 34% dry matter increase of water celery in the biological-chemical treatment (Young et al., 2003; 2004) as compared to the chemical fertilization treatment alone, indicating that at least 50% of the chemical fertilization can be saved by a complementary approach of multifunctional biofertilizers and chemical fertilizers.

Benítez-Noyola (2013) demonstrated that maize plants fertilized with 90 and 180 Kg N ha⁻¹ and inoculated with *Paenibacillus polymyxa* extracted from 20 to 28% more nitrogen and produced more grain than plants that were only chemically fertilized. These effects were explained in terms of increased root growth and nutrient availability.

Obando et al. (2013) found a statistically significant increase of 4% in the nitrogen removal by maize plants chemically fertilized (urea) and biofertilized with *Azotobacter chroococcum* AC1, with respect to plants that were only chemically fertilized.

Compared to individual application of nitrogen fertilization, Das et al. (2004) found greater N₂ nitrogen accumulation in cotton when chemical fertilization was combined with *Azotobacter* M4. The increased nitrate assimilation promoted by *Azotobacter* sp. may be related to a greater elongation of root hairs, which would improve the ability to absorb nutrients and water (Obando et al., 2013).

Dibut et al. (2009) mention that by using *Azotobacter chroococcum* they were able to reduce 30% the recommended dose of nitrogen fertilization (urea) for banana without affecting crop yield because of the atmospheric nitrogen fixing capacity of *A. chroococcum*, which they demonstrated by isotopic techniques (¹⁵N). These authors also indicate that inoculation of chickpea plants with *Mesorhizobium cicerii* resulted in beneficial effects on different parameters of growth and development, which permitted a reduction of 70% of the recommended nitrogen (urea) dose without affecting grain yield (2.05 ton ha⁻¹) as compared to control plants fertilized with 100 kg N ha⁻¹ that produced 1.98 ton ha⁻¹.

According to Biswas et al. (2000) nitrogen-fixing microorganisms can promote plant growth by transferring the fixed nitrogen to plants or by enhancing the absorption of nutrients through the modulation of the hormonal activity. In this sense, Bashan (1999) mentions that inoculation of plant growth promoting microorganisms, such as *Azospirillum* sp., results in increased accumulation of nitrogenous compounds by promoting a more effective absorption of nutrients with no apparent nitrogen fixation. Conversely, Shamsuddin (1994), using the ¹⁵N isotope technique, found that up to 89% of the N requirement of oil palm plantlets is supplied by the symbiosis with *Azospirillum*. (Mía et al., 2010)

Covarrubias-Ramírez et al. (2005) evaluated the kinetics and efficiency of P uptake in potato plants (*Solanum tuberosum* L.) cv. Alpha, through ³²P isotope technique. They demonstrated that the inoculation of *Bacillus subtilis* increased the potato biomass by 31.7%

and P uptake by 27.5%. According to the authors the increase in these variables was the result of a more developed root system, which permitted to expand the exploratory capacity of the plant in the soil.

Naveed et al. (2008) demonstrated the possibility of maintaining grain maize yields by replacing 87 Kg urea ha⁻¹ (50%) of the complete N fertilizer dose (175 Kg ha⁻¹) with 300 Kg ha⁻¹ of an organic compost elaborated with fruit and vegetable wastes and enriched with 147 g N fertilizer Kg⁻¹ compost; a basal dose of P and K (100 and 50 Kg ha⁻¹, respectively) was applied to all field plots. However, when the N-enriched compost was inoculated with different strains of *Pseudomonas* and then applied to the field plots conjunctly with 88 Kg urea ha⁻¹ a significantly increase (1.1 ton grain ha⁻¹) in the growth and yield of maize was observed over full dose of N-fertilizer and exhibited superiority over organic fertilizer (0.5 ton grain ha⁻¹). According to the authors, *Pseudomonas fluorescens* strain N3 was particularly effective in promoting growth because of its high capacity of root colonization, chitinase activity and ACC deaminase activity, characteristics that confer this strain a relatively more competitive advantage. Effects of rhizobacteria containing ACC deaminase activity are well known for improving root growth of plants as a result of reduced ethylene synthesis through ACC hydrolysis into NH₃ and α -ketobutyrate in the inoculated roots (Shaharoon et al., 2007). These results imply that inoculation of organic fertilizers with PGPR possessing these traits could help developing improved biological products combining the nutritional characteristics of the compost and the beneficial activities of the rhizobacteria with synergistic effects on growth and productivity of crops.

Khurram et al. (2012) evaluated the effect of *Bacillus* strains possessing ACC deaminase activity and phosphate solubilizing characteristics, either as a single mechanism or a dual mechanism (strains with both features). Under axenic conditions, the bacterial strains with dual plant growth-promoting activities were superior in improving growth of wheat as compared to the strains possessing single trait. Similarly, these dual traits bacterial strains were more effective than single trait strains under soil conditions (pot trial) in increasing root weight (up to 3.9-fold) and root elongation (up to 3.8-fold), dry shoot weight (up to 37.6%), number of tillers (up to 56%), grain yield (up to 38.5%) and P uptake in grain (up to 77.4%) of wheat grown in the presence of P applied as diammonium phosphate (DAP), RP (rock phosphate) or RP-enriched compost. An almost similar trend was observed when the same trial was repeated under field conditions. Inoculation in the presence of RP-enriched compost resulted in promoting various growth parameters almost comparable to that recorded in the case of DAP. It was concluded that the simultaneous presence of two superior plant growth-promoting traits in the bacteria could have an additive effect not only on growth and yield of wheat but also on P uptake. The performance of *Bacillus* strains possessing dual traits was distinctly superior to that of the single trait strains.

Abdullahi et al. (2013) studied the effect of using a biofertilizer (containing *Azospirillum* sp. and *Glomus mosseae*) and poultry manure (PM) on nutrient uptake, plant growth and soil microbial population associated with sesame under field conditions. Plant height, numbers of leaves/plant, numbers of branches/plant, leaf area, shoots and root dry biomass increased significantly due to the application of the biofertilizer and poultry manure singly or in combination over control. Combined application of the biofertilizer and poultry manure at 5 ton/ha (bio-organic treatment) significantly produced the plants with the best growth parameters, nutrient content, and N, P, and K uptakes, and also recorded the highest populations of *Azospirillum* sp. (28.56 X 10⁶ CFU g⁻¹ soil) and AM fungi (69.3 AM spores g⁻¹ soil).

¹ soil). The positive responses observed in the growth of inoculated plants may be due to the provision of nutrients, especially nitrogen, and growth promoting hormones by *Azospirillum* sp. and greater uptake of phosphorus and other nutrients due to mycorrhizal colonization (Zaidi et al., 2004). The greater availability of nutrients can be attributed to organic manure decomposition or transformation of inorganic substances into available forms by microorganisms. The increased population of *Azospirillum* sp., as well as spore density and *G. mosseae* colonization could be related to the application of manure, which constitutes a carbon source for microbes.

CONCLUSION

The information presented in this chapter shows that plant growth promoting microorganisms can be successfully used as complementary tools to organic and chemical fertilization for improving plant nutrition. It is clear that the confidence of the studies conducted under field conditions will largely depend not only on our knowledge of the nutrient and biological charge of the soil and composts or manures employed as organic fertilizers, and the growth promoter activities of the microorganisms employed as biofertilizers, but also on their particular interactions. This knowledge will be instrumental in the implementation of successful, low-environmental impact and more profitable agriculture production systems (organic or conventional).

Current and predicted costs of chemical fertilizers and cumulative evidence of negative effects of agrochemicals on the environment and human health will follow redirecting the efforts of crop research to look for the implementation of an integrated plant nutrition system in the agricultural production systems. Certainly, environmental and health, but mainly economic concerns will greatly impulse this approach in the next years.

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