

Chapter 16

Can *Bacillus* Species Enhance Nutrient Availability in Agricultural Soils?

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Abstract One major challenge for the twenty-first century will be the production of sufficient food for the global human population. The negative impacts on soil–plant–microbes–environmental sustainability due to injudicious use of chemical fertilizer, pesticide, insecticide, etc. by the unaware farmers deteriorate soil and environment quality. One possible way to use efficient soil microorganisms to remediate nutrient deficiency in agricultural soils and other plant growth-promoting (PGP) activities

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that can be of help for plant growth and development. The *Bacillus* species is one the most dominant rhizospheric bacterial/rhizobacteria species like *Bacillus subtilis*, *B. cereus*, *B. thuringiensis*, *B. pumilus*, *B. megaterium*, etc. that can help enhance the plant growth and development by different mechanisms, which PGPR can inhibit phytopathogens is the production of hydrogen cyanide (HCN) and/or fungal cell wall degrading enzymes, e.g., chitinase and β -1,3-glucanase. Direct plant growth promotion includes symbiotic and non-symbiotic PGPR which function through production of plant hormones such as auxins, cytokinins, gibberellins, ethylene, and abscisic acid. Mitigate the challenge by adopting eco-friendly crop production practices. Some *Bacillus* species function as a sink for 1-aminocyclopropane-1-carboxylate (ACC), the immediate precursor of ethylene in higher plants, by hydrolyzing it into α -ketobutyrate and ammonia and in this way promote root growth by lowering indigenous ethylene levels in the micro-rhizo environment. *Bacillus* species also help in solubilization of mineral phosphates, potassium, zinc, and other nutrients; rhizobacteria retain more soil organic N and other nutrients in the soil–plant system, thus reducing the need for fertilizers and enhancing release of the nutrients from indigenous or mineral sources, enhancing the economic and environmental sustainability.

Keywords *Bacillus* spp. • Mineral solubilization • Rhizosphere • Fe sequestration • Efficient microorganisms • Nutrient uptake

16.1 Introduction

World food insecurity is a chronic problem and is likely to worsen with climate change and rapid population growth. It is largely due to poor yields of the cereal, pulse, and millet crops caused by factors including soil–plant–environment system. The world's population is assumed to increase from ~7 billion now to 8.3 billion in 2025. The world will need 70–100 % more food by 2050 (Godfray et al. 2010). The increasing human population is placing greater pressure on soil and water resources and threatening our ability to produce sufficient food, feed, and fiber. As a result, there is a growing consensus within our global community that the protection of natural resources and implementation of environmentally and economically sound agriculture practices is of the utmost priority (Ahmad et al. 2016; Bahadur et al. 2016a).

Nowadays world agriculture is facing new challenges in which ecological and molecular approaches are being integrated to achieve higher crop yields while minimizing negative impacts on the environment. In this direction, enhancing nutrient availability, plant growth and yield, and plant multi-stress resistances are key strategies. Root-, soil-, and plant-associated eco-friendly numerous microorganisms produce plant growth-promoting activities with specific action against coexisting microorganisms toward the soil sustainability (Raaijmakers et al. 2009; Combes-Meynet et al. 2011; Genilloud et al. 2011; Pineda et al. 2012; Meena et al. 2013; Maurya et al. 2014; Kumar et al. 2015; Verma et al. 2015b). Global agriculture has to double food production by 2050 in order to feed the world's growing population and at the same time reduce its reliance on mineral/inorganic agricul-

tural inputs. To achieve this goal, there is an urgent need to harness the multiple beneficial interactions that occur between soil microorganisms, plant, and the environment. Beneficiary impacts of soil microorganisms enhance the sustainability of soil–plant–environment ecosystem (Gupta 2012; Bahadur et al. 2016b; Das and Pradhan 2016; Dominguez-Nuñez et al. 2016).

16.2 Soil Microbial Diversity

The beneficial influences of soil microorganisms on plant growth and development include nitrogen fixing (Peix et al. 2001; Riggs et al. 2001; Marino et al. 2007), phosphorus solubilization (Yasmin et al. 2004; Tajini et al. 2012; Verma et al. 2013), potassium solubilization (Phua et al. 2012; Yadegari et al. 2012; Zhang et al. 2013; Meena et al. 2014; Maurya et al. 2014; Saha et al. 2016a), zinc solubilization (Mäder et al. 2010; Saravanan et al. 2007; Bahadur et al. 2016b), and indirect mechanisms such as production of phytohormones (Rashedul et al. 2009; Abbasi et al. 2011) such as auxins (Verma et al. 2013), siderophores (Filippi et al. 2011; Yu et al. 2011a, b), and PGPR from the rhizosphere to screen for their growth-promoting activity in plants under axenic conditions (Datta et al. 2011; Meena et al. 2015a, 2016; Singh et al. 2015; Verma et al. 2015a;).

16.2.1 Agricultural Important Soil Microorganisms

It has been reported that biological fertilization is an efficient method to supply plants with their necessary nutrients. It is economically and eco-friendly recommendable, because its results improved the agricultural and environmental sustainability. During the past century, industrialization of agriculture has provoked a significant and essential productivity increase, which has led to a greater amount of food available to the general population. Along with this abundance, the appearance of serious environmental and social problems came with the package: problems that must be faced and solved in the not too distant future. Nowadays, it is urgent to maintain that high productivity, but it is becoming urgent to alter as little as possible the environment. Clearly we must then head for a more environmentally sustainable agriculture while maintaining ecosystems and biodiversity. One potential way to decrease negative environmental impact resulting from continued use of chemical fertilizers, herbicides, and pesticides is the use of plant growth-promoting rhizobacteria (PGPR). This term was first defined by Kloepper and Schroth (1978) to describe soil bacteria that colonize the rhizosphere of plants, growing in, on, or around plant tissues that stimulate plant growth by several mechanisms. Since that time, research activities aimed at understanding how these bacteria perform their positive (or negative) effect have steadily increased, and many reports have been published on these microorganisms. Although interactions between soil microorganisms, plants–rhizosphere, and the environment have important consequences for

ecosystem dynamics and changes in plant communities with time occur in concert with changes in soil properties, the relationships between soil microbial community and plant community dynamics are not fully understood (Van Der Putten 2003; Saha et al. 2016b). Plants are able to modify the structure of microbial communities in their rhizosphere (Berg and Smalla 2009), while soil microbes are important regulators of plant productivity, both through direct effects and through regulation of nutrient availability (Meena et al. 2014). However, the role of such interactions in plant community dynamics with time has received little attention (Bartelt-Ryser et al. 2005; Meena et al. 2015b, c).

16.2.2 *The Bacillus Diversity in Agricultural Soils*

Bacillus is the most abundant genus in the rhizosphere, and the PGPR activity of some of these strains has been known for many years, resulting in a broad knowledge of the mechanisms involved (Probanza et al. 2002; Mañero et al. 2003). Naturally present in the immediate vicinity of plant roots, *B. subtilis* is able to maintain stable contact with higher plants and promote their growth (Dotaniya et al. 2016; Jaiswal et al. 2016; Jha and Subramanian 2016). In a micro-propagated plant system, bacterial inoculation at the beginning of the acclimatization phase can be observed from the perspective of the establishment of the soil microbiota rhizosphere. *B. licheniformis* when inoculated on tomato and pepper shows considerable colonization and can be used as a bio-fertilizer without altering normal management in greenhouses as well as field condition (Bacon et al. 2001; Sessitsch et al. 2002; Wu et al. 2005). *B. megaterium* is very consistent in improving different root parameters in mint. Phosphorus-solubilizing bacteria (PSB) *B. megaterium* var. *phosphaticum* (Lavakusha et al. 2014) and potassium-solubilizing bacteria (KSB) *B. mucilaginosus* (Meena et al. 2014; Maurya et al. 2014) when inoculated in nutrient-limited soil showed that rock materials (P and K rocks) and both bacterial strains consistently increased mineral availability, uptake, and plant growth of pepper and cucumber, suggesting its potential use as bio-fertilizer (Han et al. 2006; Supanjani et al. 2006).

Soil is the main reservoir of the potential bacterial rhizosphere community (Berg and Smalla 2009). Evidence is increasing that plants actively select specific elements of their bacterial rhizosphere micro-flora, establishing a habitat which is favorable for the soil–plant–environment system (Robin et al. 2007; Houlden et al. 2008; Rudrappa et al. 2008). The soil–matrix is a favorable niche for bacteria since both temperature and humidity are relatively sustainable (Ranjard et al. 2000; Sessitsch et al. 2001), mineral composition (Carson et al. 2009), and agricultural practices (Rooney and Clipson 2009; Saha et al. 2016b). The neutral soil reaction is the most favorable condition for higher bacterial diversity, whereas acidic soils were least diverse; it's favorable for fungus growth and development. Bacterial population revealed by culture-dependent techniques represents only 1–10 % of the total bacterial micro-flora present in soil and is now known as the great plate count anomaly (Amann et al. 1995; Meena et al. 2015d, e).

16.2.3 Soil–Plant–Microbe System

Soil–plant–microbe interactions in the rhizosphere soils are responsible for various processes that influence plant growth and development and nutrient mobilization (Awasthi et al. 2011; Singh 2013); a wide range of beneficial microorganisms (e.g., bacteria, fungi, and actinomycetes) associated with plant roots have the ability to promote the growth of the host plant under natural as well as agroecosystem by various mechanisms, namely, fixation of atmospheric nitrogen (Glick et al. 2007), phosphorus (Verma et al. 2012a), potassium (Zhang et al. 2013), and zinc solubilization (Bapiri et al. 2012), and production of plant growth regulators (Meena et al. 2012; Miransari 2011; Rajkumar et al. 2012; Verma et al. 2012b). Besides, the plant-associated microbes residing in the rhizosphere enhance the mobility and availability of plant nutrients to the plants through release of chelating agents, acidification, and redox changes (Glick et al. 2007; Rajkumar et al. 2012). It is also well known that these microbes can utilize the plant-derived substances (e.g., root exudates) comprising different compounds (e.g., organic acids, sugars, vitamins, and amino acids) as major nutrients for their growth and development (Berendsen et al. 2012; Dakora and Phillips 2002; Ryan et al. 2001). On the other side, plants stimulate or inhibit the growth of specific microorganisms through releasing secondary metabolites (e.g., pyrones, sesquiterpenes) into the rhizosphere (Reino et al. 2008; Berendsen et al. 2012; Chakraborty et al. 2012). An example of bacterial stimulation of maize plant root shoot growth is shown in Fig. 16.1.

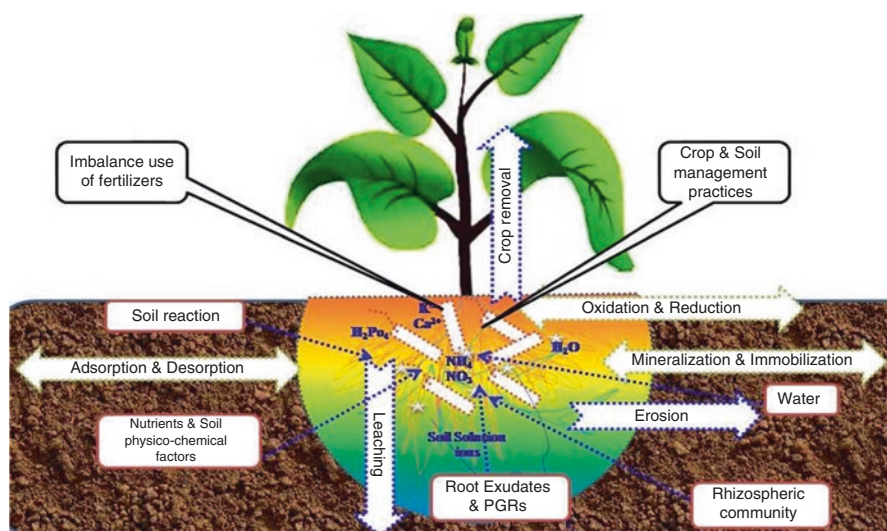


Fig. 16.1 Schematic illustration of how soil and crop management practice factors influence nutrient availability under soil–plant system

16.3 Current Nutrient Status of Agricultural Soils

A recent review of worldwide data on N use efficiency for cereal crops from researcher-managed experimental plots reported that single-year fertilizer N recovery efficiencies are ~65 % for corn, ~57 % for wheat, and ~46 % for rice. Differences in the scale of farming operations and management practices (i.e., tillage, seeding, weed and pest control, irrigation, harvesting) usually result in lower nutrient use efficiency (Kumar et al. 2016; Masood and Bano 2016; Meena et al. 2016). Nitrogen recovery in crops grown by farmers rarely exceeds ~50 % and is often much lower. A review of best available information suggests average N recovery efficiency for fields managed by farmers ranges from about 20 % to 30 % under rainfed conditions and 30 to 40 under irrigated conditions. Looked at N fertilizer recovery under different cropping systems and reported 37 % recovery for corn grown in the north central USA. They found N recovery averaged 31 % for irrigated rice grown by Asian farmers and 40 % for rice under field-specific management. In India, N recovery averaged 18 % for wheat grown under poor weather conditions, but 49 % when grown under good weather conditions (von Braun 2007; Rajkumar and Freitas 2008a, b; Khamna et al. 2010). Phosphorus (P) efficiency is also of interest because it is one of the least available and least mobile mineral nutrients. First year recovery of applied fertilizer P ranges from less than 10 % to as high as 30 % (Fig. 16.2).

However, because fertilizer P is considered immobile in the soil and reaction (fixation and/or precipitation) with other soil minerals is relatively slow, long-term recovery of P by subsequent crops can be much higher. There is little information available about potassium (K) use efficiency. However, it is generally considered to have higher use efficiency than N and P because it is immobile in most soils and is not subject to the gaseous losses that N is or the fixation reactions that affect P. First year recovery of applied K can range from 20 % to 60 % (Fig. 16.3).

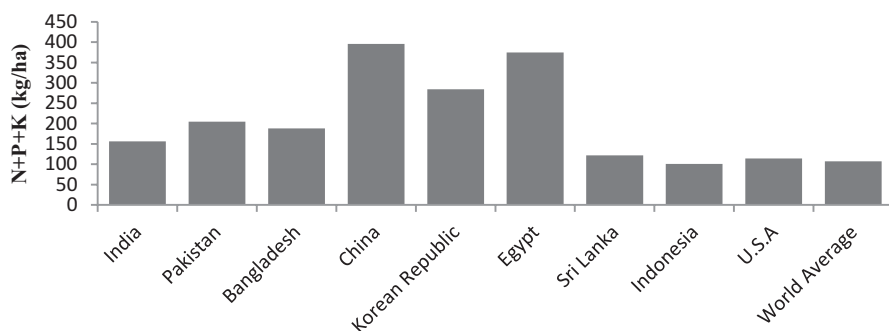


Fig. 16.2 The worldwide nutrients (NPK) consumption in agricultural production system

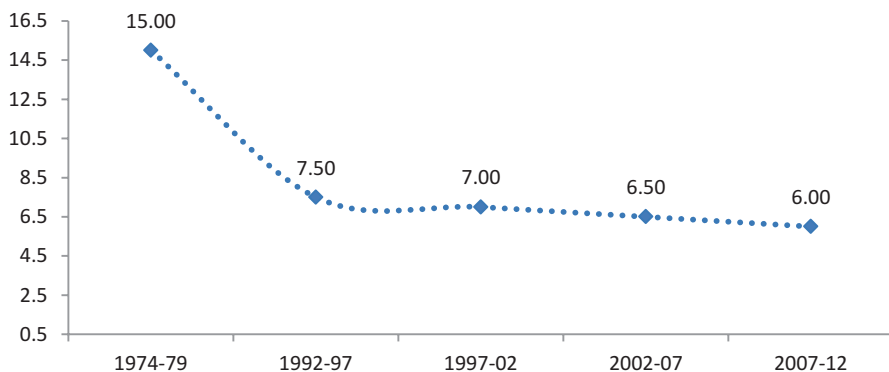


Fig. 16.3 Crop response to fertilizer (kg of food grain/kg NPK)

16.4 PGPR Mechanism of *Bacillus* Species

Bacillus species have the potential to act as a PGPR, nutrient solubilization, and bioremediation, to enhance crop growth, yield, and nutrient uptake by different mechanisms that contributed through direct and indirect mechanisms in the development of sustainable soil–plant–environment systems (Schippers et al. 1995). The generally plant growth-promoting bacteria function in three different ways – synthesizing particular PGR compounds for the growth and development of plants (Zahir et al. 2004), facilitating the mineralization or solubilization of mineral from fixed form to plant available form or soil solution that can help to enhance the nutrients’ uptake from the soil (Cakmakci et al. 2006), and helping to reduce the chances of disease infection or preventing the agricultural crops from insect, pest, and diseases (Raj 2004; Saravanakumar et al. 2008; Meena et al. 2015f; Prakash and Verma et al. 2016; Priyadharsini and Muthukumar 2016).

16.4.1 Direct and Indirect Mechanisms

The mechanisms of PGPB-mediated enhancement of plant growth and yield of many crops are not yet fully understood (Dey et al. 2004). However, possible explanations include (a) the ability to produce a vital enzyme, 1–aminocyclopropane–1–carboxylate (ACC) deaminase, to reduce the level of ethylene in the root of developing plants thereby increasing the root length and growth (Li et al. 2006; Meena et al. 2013; Verma et al. 2013); (b) the ability to produce hormones like auxin, i.e., indole acetic acid (IAA) (Patten and Glick 2002), abscisic acid (ABA) (Dangar and Basu 1987; Dobbelaere et al. 2003), gibberellic acid (GA), and cytokinins (Dey et al. 2004); (c) a symbiotic nitrogen fixation (Kennedy et al. 2004); (d) antagonism against phytopathogenic bacteria by producing siderophores, β -1,3-glucanase, chitinases, antibiotic, fluorescent pigment, and cyanide (Cattelan et al. 1999; Pal et al. 2001; Glick and

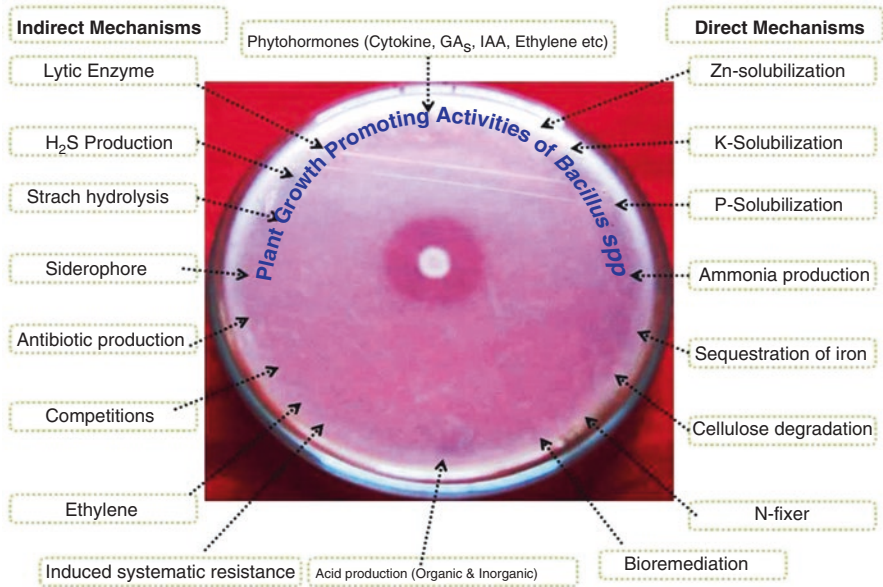


Fig. 16.4 Mechanism of plant growth-promoting *Bacillus* species. (a) Direct mechanism (e.g., N₂-fixer, phosphorus, potassium and zinc solubilization, etc.). (b) Indirect mechanism (e.g., IAA, GAs, cytokinins and certain VOCs, etc.), both mechanism enhance plant mineral uptake and productivity of crop

Stearns 2011); (e) solubilization and mineralization of nutrients, particularly mineral phosphates and potassium (Maurya et al. 2014; Lavakusha et al. 2014; Meena et al. 2014); (f) enhanced abiotic stress (Saleem et al. 2007; Stajner et al. 1997); and (g) production of water-soluble B group vitamins such as niacin, pantothenic acid, thiamine, riboflavin, and biotin (Revillas et al. 2000; Zhuang et al. 2007; Raghavendra et al. 2016; Rawat et al. 2016; Saha et al. 2016a) (Fig. 16.4).

16.4.2 Nitrogen Fixer

The mineralization of soil organic nitrogen (N) through nitrate to gaseous N₂ by soil microorganisms is a very important process in global N cycling. This cycle includes N mineralization, nitrification, denitrification, and N₂ fixation. A number of bacterial species belonging to the genera *Bacillus*, *Azospirillum*, *Alcaligenes*, *Arthrobacter*, *Acinetobacter*, *Burkholderia*, *Enterobacter*, *Erwinia*, *Flavobacterium*, *Pseudomonas*, *Rhizobium*, and *Serratia* (Yu et al. 2012; Braghini Sa et al. 2012; Thepsukhon et al. 2013) are associated with the plant rhizosphere and are able to exert a beneficial effect on plant growth and development. Nowadays new techniques have identified a wide range of organisms with the plant rhizosphere with the capacity to carry out biological nitrogen fixation (BNF) – greatly expanding our appreciation of the

diversity and ubiquity of N fixers – but our understanding of the rates and controls of BNF at ecosystem and global scales has not advanced at the same pace. Nevertheless, determining rates and controls of BNF is crucial to placing anthropogenic changes to the N cycle in context and to understanding, predicting, and managing many aspects of global environmental change. Here, we estimate terrestrial BNF for a preindustrial world by combining information on N fluxes with ^{15}N relative abundance data for terrestrial ecosystems. Our estimate is that preindustrial N fixation was 58 (range of 40–100) TgN fixed yr⁻¹; adding conservative assumptions for geological N reduces our best estimate to 44 TgN yr⁻¹. This approach yields substantially lower estimates than most recent calculations; it suggests that the magnitude of human alteration of the N cycle is substantially larger than has been assumed (Saha et al. 2016b; Sharma et al. 2016; Shrivastava et al. 2016).

16.4.3 Phosphorus Solubilizers

The role of phosphorus mobilizers and solubilizers is more important in soil–plant system because only ~15 % of the phosphorus fertilizer is directly available to the plant growth and development and the rest of the 85 % is lost by different processes like runoff and P fixation due to unfavorable soil conditions. However, eminent soil fertility scientists recognize that soil reactions with applied phosphate limit its direct uptake by plants in the short term; the long-term recovery can approach 90 %, because phosphorus is retained in the soil in slowly available forms (Syers 2003; Panhwar et al. 2012).

Phosphate solubilization by rhizospheric microorganisms in mineral phosphate solubilization was known as early as 1903. Since then, there have been extensive studies on the mineral phosphate solubilization by naturally abundant rhizospheric microorganisms (Fig. 16.5). Strains from bacterial genera *Pseudomonas*, *Bacillus*, *Rhizobium*, and *Enterobacter* along with *Penicillium* and *Aspergillus* fungi are the most powerful P solubilizers (Whitelaw 2000). *B. megaterium*, *B. circulans*, *B. subtilis*, *B. polymyxa*, and *B. sircalmous* could be referred as the most important strains (Verma et al. 2013; Meena et al. 2014; Yu et al. 2012).

16.4.4 Potassium Solubilizers

K-solubilizing bacteria are able to release potassium from insoluble minerals (Sugumaran and Janarthanam 2007; Basak and Biswas 2009, 2012; Kalaiselvi and Anthoniraj 2009; Parmar and Sindhu 2013; Zarjani et al. 2013; Prajapati et al. 2013; Zhang et al. 2013; Gundala et al. 2013; Archana et al. 2012, 2013; Sindhu et al. 2012). In addition, researchers have discovered that K-solubilizing bacteria can provide beneficial effects on plant growth through suppressing pathogens and improving soil nutrients and structure. For example, certain bacteria can weather silicate minerals to release potassium, silicon, and aluminum and secrete bioactive

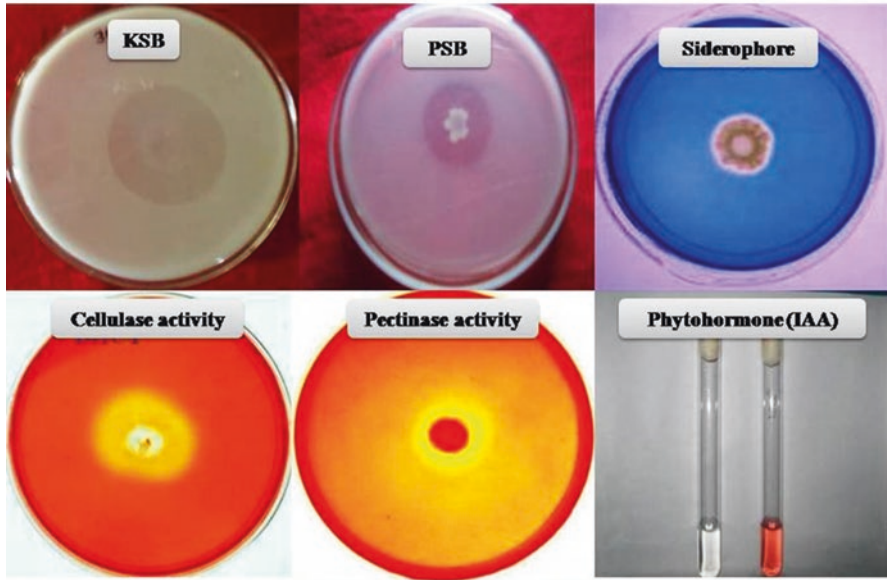


Fig. 16.5 The plant growth-promoting activities of *Bacillus* species, like potassium-solubilizing bacteria (*KSB*), phosphorus-solubilizing bacteria (*PSB*), iron-sequestering bacteria (siderophore-producing bacteria), cellulose-degrading activities, pectinase-producing bacteria, and phytohormone-producing bacteria (IAA, GA₃, ethylene, etc.)

materials to enhance plant growth (Fig. 16.5). These bacteria are widely used in biological K fertilizers and biological leaching (Lian et al. 2002; Bosecker 1997). The considerable populations of potassium-solubilizing microorganisms are present in rhizospheric soil which promotes the plant growth (Sperberg 1958).

It is generally accepted that the major mechanism of mineral K solubilization is the action of organic acids synthesized by rhizospheric microorganism. Productions of organic acids result in acidification of the microbial cell and its surroundings environment which promote the solubilization of mineral K. Silicate bacteria were found to resolve potassium, silicon, and aluminum from insoluble minerals. Silicate bacteria exert beneficial effects upon plant growth and yield. The KSB can promote K solubilization from silicate mineral and is very important to enhance the fertility status of soils. Rhizospheric microorganisms contribute directly and indirectly to the physical, chemical, and biological parameters of soil through their beneficial or detrimental activities (Meena et al. 2015g, h; Sindhu et al. 2016; Teotia et al. 2016).

16.4.5 Zinc Solubilizers

Zinc is predominantly taken up as a divalent cation, Zn²⁺, but in some cases of calcareous and high pH, it is believed to be taken up as a monovalent cation ZnOH⁺. Zinc interactions in both plants and soils are quite complex and play a major role in

how and when we should apply zinc to a crop. Increasing the Zn and Fe concentration of food crop plants, resulting in better crop production and improved human health is an important global challenge. Among micronutrients, Zn deficiency is occurring in both crops and humans (White and Zasoski 1999; Welch and Graham 2004). Zinc is required in relatively small concentrations in plant tissues (5–100 mg/kg). Zn deficiency is well reported in the soils of much of the world. The deficiency of Zn in cereals especially rice is nutritionally a major problem. Cereals play in satisfying daily calorie intake in the developing world, but the Zn concentration in the grain is inherently very low, particularly when grown on Zn-deficient soils.

The major reason for the widespread occurrence of zinc deficiency problems in crop plant is the low solubility of Zn in soils rather than low total amount of Zn. Zinc-solubilizing bacteria (ZSB) help to solubilize the fixed form of Zn and increase uptake of Zn leading to fortification of grains with Zn (Bapiri et al. 2012). Soil microorganisms require various nutrients for their growth and metabolism. Among the nutrients, zinc is an element present in the enzyme system as cofactor and metal activator of many enzymes (Parisi and Vallee 1969). This causes transformation of about 96–99 % of applied available zinc to various unavailable forms (Fig. 16.5). The zinc thus made unavailable can be reverted back to available form by inoculating a bacterial strain capable of solubilizing it. Since zinc is a limiting factor in crop production, importance of ZSB has an immense in zinc nutrition to plants (Bapiri et al. 2012; Verma et al. 2013).

16.4.6 Fe Sequestration

Iron (Fe) deficiency is a worldwide problem that is directly correlated with poverty and food insecurity. Approximately one third of the world's population suffers from Fe deficiency-induced anemia, 80 % of which are in developing countries (Boccio and Iyengar 2003; Miethke and Marahiel 2007). Total Fe content in soil is relatively high, but its availability to soil microorganisms is low in aerated soils because the prevalent form (Fe^{3+}) is poorly soluble. Plants and microorganisms have developed mechanisms to increase Fe uptake (Marschner 1995; Rajkumar et al. 2010). In plants, there are two different strategies in response to Fe deficiency. Strategy I plants (dicots and non-graminaceous monocots) release organic acid anions which chelate Fe. Iron solubility is also increased by decreasing the rhizosphere pH, and Fe uptake is enhanced by an increased reducing capacity of the roots ($\text{Fe}^{3+} \rightarrow \text{Fe}^{2+}$). Strategy II plants (*Poaceae*) release phytosiderophores that chelate Fe^{3+} (Von Wiren et al. 1993; Sinha and Mukherjee 2008; Sullivan et al. 2012). Under Fe deficiency stress, soil microorganisms release organic acid anions or siderophores that chelate Fe^{3+} . After movement of the ferrated chelate to the cell surface, Fe^{3+} is reduced either outside or within the cell (Neilands 1984). Microorganisms produce a range of siderophores, e.g., ferrichromes by fungi and enterobactin, pyoverdine, and ferrioxamines by bacteria (Von Wiren et al. 1993; Ma et al. 2011). Rhizobacterial strain significantly influences Fe uptake by agricultural crop (Yu et al. 2011a, b; Sadeghi et al. 2012; Socha and Guerinot 2014).

Fe was supplied either as microbial siderophores (pseudobactin [PSB] or ferrioxamine B [FOB]) or as phytosiderophores obtained as root exudates from barley (epi-3-hydroxy-mugineic acid [HMA]) under varied population densities of rhizosphere microorganisms (axenic, uninoculated, or inoculated with different microorganism cultures). When maize was grown under axenic conditions and supplied with FeHMA Socha and Guerinot 2014), Fe uptake rates were 100–300 times higher compared to those in plants supplied with Fe siderophores (Fig. 16.5). Fe from both sources was taken up without the involvement of an extracellular reduction process. The supply of FeHMA enhanced both uptake rate and translocation rate to the shoot (>60 % of the total uptake). However, increased density of microorganisms resulted in a decrease in Fe uptake rate (up to 65 %), presumably due to microbial degradation of the FeHMA. In contrast, when FeFOB or FePSB was used as the Fe source, increased population density of microorganisms enhanced Fe uptake. The enhancement of Fe uptake resulted from the uptake of FeFOB and FePSB by microorganisms adhering to the rhizoplane or living in the free space of cortical cells. The microbial apoplasmic Fe pool was not available for root to shoot transport or, thus, for utilization by the plants (Socha and Guerinot 2014). These results, in addition to the low uptake rate under axenic conditions, are in contrast to earlier hypotheses suggesting the existence of a specific uptake system for Fe siderophores in higher plants. The bacterial siderophores PSB and FOB were inefficient as Fe sources for plants even when supplied by stem injection. It was concluded that microorganisms are involved in degradation processes of microbial siderophores, as well as in competition for Fe with higher plants (Crowley et al. 1992; Socha and Guerinot 2014).

Fe sequestration of *B. megaterium* in iron-deficient medium detected in the exponential phase of growth seems not to be affected by the glucose availability and was not related with the onset of endospore formation (Chincholkar et al. 2007). The carbon source affected the siderophore production by *B. megaterium* (Socha and Guerinot 2014). Among the carbon sources tested, the growth on glycerol promoted the highest siderophore production. The increase of arginine concentration in the culture medium did not enhance the siderophore production. The agitation had a positive effect on the growing of *B. megaterium* and siderophore production. To our knowledge, this is the first work that describes the physiological response of *B. megaterium* in terms of siderophore production (Das et al. 2007; Socha and Guerinot 2014).

16.5 Impact of *Bacillus* Species on Yield and Nutrient Uptake

Nowadays rapidly increasing rate of human population with reducing land holding size due to urbanizations, industrialization, and modernization, by all these increasing pressure how to we increasing our food grain production in compared to population with soil–plant–environment sustainability (Ilippi et al. 2011; Sullivan et al. 2012). One possible way to use of beneficially agricultural important microorganisms, with judicious application of mineral as well as chemical fertilizer for sustainable crop production. In

this context many research studies reported that *Bacillus* species and other rhizobacterial strains inoculated to soil significantly enhanced crop growth, yield, and nutrient uptake (Yasmeen et al. 2012b; Velázquez et al. 2016; Yadav et al. 2016).

Bacillus spp. are used as PGPR with plant growth-promoting traits like phosphate, potassium, and zinc solubilization; N₂ fixation and phytohormone production (Liu et al. 2006; Lavakusha et al. 2014; Meena et al. 2014; Maurya et al. 2014) are also being used as bio-inoculants for crop production. The *Bacillus* species are reported to increase the yield in wheat (de Freitas et al. 2007; Cakmakci et al. 2007), maize (Pal et al. 2001), sugar beet (Cakmakci et al. 2006), and spinach (Cakmakci et al. 2007). According to Verma et al. (2012a) observed increase in growth and yield of beans by co-inoculating *Bacillus* strains with other rhizobacteria significantly influenced on nodule formation in pulse crops (Lavakusha et al. 2014; Liu et al. 2006; Yadav et al. 2010) and are widely used as plant health-promoting rhizobacteria by reducing diseases and producing antibiotic (Verma et al. 2013) (Table 16.1).

16.6 Implications of Efficient Soil Microorganisms in Sustainable Agriculture

The various ways in which efficient soil microorganisms have been used over the past fifth decade to modern sustainable technology, human and animal health, food processing, food safety and quality, genetic engineering, environmental protection, agricultural biotechnology, and in more effective treatment of agricultural. However, microbial technologies have been applied to various agricultural and environmental problems with considerable success in recent years; they have not been widely accepted by the scientific community as it is often hard to consistently reproduce their beneficial effects. We can enhance soil–plant–environment sustainability through the use of efficient soil microorganisms for sustainable agricultural production (Godfray et al. 2010). As discussed above, agriculture should consider maximizing the coadaptation between soil–plant–microbes in an effort to promote soil microbial diversity (Badri et al. 2008 ; Yasin et al. 2016; Zahedi 2016).

Which implications does decoupling the coadapted soil–plant–microbial relationship have on sustainable agriculture? The soil environment is likely the most complex biological community. Efficient soil organisms are extremely diverse and contribute to a wide range of ecosystem services that are essential to the sustainable function of natural and managed ecosystems. The efficient soil organism community can have direct and indirect impacts on land productivity. Direct impacts are those where specific efficient soil microorganisms affect crop yield immediately (Broeckling et al. 2008). Indirect effects include those provided by soil organisms participating in carbon and nutrient cycles, soil structure modification, and food web interactions that generate ecosystem services that ultimately affect productivity. Research opportunities and gaps related to methodological, experimental, and conceptual approaches may be helpful to enhance sustainable agricultural production system.

Table 16.1 Impact of *Bacillus* species on growth, yield, nutrient uptake, and plant growth-promoting activities with different crop species

Crop species	<i>Bacillus</i> species	Impact	References
<i>Cicer arietinum</i>	<i>B. firmus</i> strain NARS1	Cold stress	Khan et al. (2007)
	<i>B. megaterium</i>	Phytohormones	Verma et al. (2012b)
<i>Lolium multiflorum</i>	<i>B. pumilus</i> C2A1	Bioremediation	Ahmad et al. (2006)
<i>Cucumis melo</i>	<i>B. subtilis</i> Y-IV	Plant growth, root colonization	Zhao et al. (2011)
<i>Triticum aestivum</i>	<i>B. pumilus</i> strain S2	Enhance growth, yield, nutrient uptake	Abbasi et al. (2011)
	<i>B. pumilus</i> S6-05		Upadhyay et al. (2009)
<i>Atriplex lentiformis</i>	<i>B. pumilus</i> ES4	Phyto-stabilization	De-Bashan et al. (2008)
<i>Glycine max</i>	<i>B. subtilis</i> CICC1016	Siderophore, P solubilization, antagonism with <i>F. oxysporum</i> , <i>S. rolfsii</i> , <i>R. solani</i>	Wahyudi et al. (2011)
	<i>B. sphaericus</i> NUC-5		
	<i>B. cereus</i> strain SS-07		
	<i>B. pumilus</i>		
<i>Oryza sativa</i>	<i>B. pumilus</i> strain S68	ACC producing, PGRs	Lavakush et al. 2014
	<i>B. sp</i> SB1-ACC3		
<i>Artemisia annua</i>	<i>B. subtilis</i> strain Daz26	Nitrogen fixing	Awasthi et al. (2011)
<i>Fragaria</i> spp.	<i>B. subtilis</i> NA-101	IAA equivalents, siderophore, strawberry root, and shoot growth	Pereira et al. (2011)
	<i>B. subtilis</i> NA-120		
<i>Solanum tuberosum</i>	<i>B.</i> strain	Phosphorus solubilization, IAA	Calvo et al. (2010)
<i>Zea mays</i>	<i>B. sp.</i>	Seed germination and root shoot growth	Ngoma et al. (2014)
<i>Prunus cerasus</i> cv. <i>Kutahya</i>	<i>B. subtilis</i> OSU – 142	Fruit set, pomological and chemical characteristics, color values	Karakurt et al. (2011)
	<i>B. megaterium</i> M		
<i>Piper nigrum</i>	<i>B. subtilis</i> CAS15	Siderophore producing	Yu et al. (2011a)
<i>Lycopersicon esculentum</i>	<i>B. amyloliquefaciens</i> QL5	Controlling bacterial wilt	Wei et al. (1996)
	<i>B. amyloliquefaciens</i> QL18		
<i>Juglans</i> spp.	<i>B. megaterium</i>	Nitrogen fixing, PSB	Yu et al. (2012)
<i>Lycopersicon esculentum</i>	<i>B. subtilis</i>	Antifungal, nutrient availability	Nihorimbere et al. (2010)
<i>Mammillaria fraileana</i>	<i>B. megaterium</i> MIPC4	Mobilization of elements from rocks, mineral degradation	Lopez et al. (2012)
			Puente et al. (2009a, b)

(continued)

Table 16.1 (continued)

Crop species	<i>Bacillus</i> species	Impact	References
<i>Zea mays</i>	<i>B. mojavensis</i>	Maize seedling growth and nutrient uptake	Bahadur et al. (2016b)
<i>Bouteloua dactyloides</i>	<i>B. spp.</i>	Phytoremediation, PGPR	Ma et al. (2011)
<i>Zea mays</i>	<i>B. spp.</i>	Drought tolerant	Singh et al. (2013)
<i>Brassica juncea</i>	<i>B. spp.</i> Ba32	PGRs, P solubilization	Rajkumar et al. (2006) Rajkumar et al. (2008a, b)
<i>Brassica juncea</i>	<i>B. subtilis</i> SJ-101	IAA, P solubilization, increased shoot length, fresh and dry weights	Zaidi et al. (2006) Rajkumar et al. (2008)
<i>Brassica napus</i>	<i>B. subtilis</i> RJ16 (RS)	IAA, Cd-mobilization, increased root elongation (gnotobiotic conditions), shoot and root dry weight (pot experiment)	Sheng and He (2006) Rajkumar et al. (2009)
<i>Sorghum bicolor</i>	<i>B. subtilis</i> <i>B. pumilus</i>	Increase root shoot biomass	Abou-Shanab et al. (2008)
<i>Lycopersicon esculentum</i>	<i>B. amyloliquefaciens</i> S499	PGPR, P solubilization	Nihorimbere et al. (2011)
<i>Sorghum bicolor var. sudanense</i>	<i>B. mucilaginosus</i>	Potassium solubilizing	Basak and Biswas (2010)
<i>Glycine max</i>	<i>B. subtilis</i>	Nutrient uptake, plant growth	Bais et al. (2002)
<i>Pinus thunbergii</i>	<i>B. cereus</i>	Growth, nutrient uptake	Wu et al. (2011)
<i>Actinidia deliciosa</i>	<i>B. subtilis</i> OSU142, <i>B. megaterium</i> RC01	Rooting and root growth	Erturk et al. (2010)
<i>Musa paradisiaca</i>	<i>B. amyloliquefaciens</i> W19	<i>Fusarium</i> wilt and plant growth, increased biomass	Baset Mia et al. (2010)
<i>Brassica napus</i>	<i>B. licheniformis</i> BLMB1	Cr, Cu, Pb, and Zn phytoextraction	Brunetti et al. (2011) Rajkumar et al. (2010)
<i>Triticum aestivum</i>	<i>B. subtilis</i>	PGRs, nutrient uptake	Upadhyay et al. (2011, 2012)
<i>Zea mays</i>	<i>B. megaterium</i>	Vegetative growth, yield	Singh et al. (2013)
<i>Arabidopsis thaliana</i>	<i>B. subtilis</i>	P solubilization, PGRs	Zhang et al. (2008)
<i>Persea gratissima</i>	<i>B. megaterium</i>	Phytohormones, growth, yield	Nadeem et al. (2012)
<i>Raphanus sativus</i>	<i>B. subtilis</i> , <i>B. megaterium</i>	Bioremediation, yield, PGRs	Kaymak et al. (2009)
<i>Medicago sativa</i>	<i>B. pumilus</i> <i>B. licheniformis</i>	Growth, yield, nutrient uptake	Medina et al. (2003)

(continued)

Table 16.1 (continued)

Crop species	<i>Bacillus</i> species	Impact	References
<i>Lycopersicon esculentum</i>	<i>B. megaterium</i>	PGRs, growth, yield	Singh et al. (2013)
<i>Manihot esculenta</i> Crantz	<i>B. megaterium</i> Cav. cy3	P solubilization	Chen et al. (2014)
<i>Oryza sativa</i>	<i>B. circulans</i> P2	Increased rice grain yield	Panhwar et al. (2012)
	<i>B. megaterium</i> P5		
<i>Spinacia oleracea</i>	<i>B. megaterium</i> RC07	PGRs, vegetative growth, bioremediation	Çakmakçı et al. (2007)
	<i>B. subtilis</i> RC11		
<i>Sorghum bicolor</i>	<i>B. polymyxa</i>	Increased grain and dry matter yields and N and P uptake	Alagawadi and Gaur (1992)
<i>Cicer arietinum</i>	<i>B. megaterium</i>	Increased dry matter, grain yield and P uptake, nodulation, N fixation	Verma et al. (2013)
<i>Helianthus annuus</i>	<i>B. megaterium</i> M-13	Increased yield, oil, protein content	Ekin (2010)
<i>Solanum tuberosum</i>	<i>B. polymyxa</i>	Increased yield, P uptake	Kundu and Gaur (1980)
<i>Rubus idaeus</i>	<i>B. megaterium</i>	Increased crop yield	Orhan et al. (2006)
<i>Ammi visnaga</i>	<i>B. simplex</i>	Increased root, shoot length, dry weight	Hassen et al. (2010)
	<i>B. cereus</i>		
<i>Fragaria ananassa</i>	<i>B. megaterium</i>	Increased fruit yield, nutrient contents	Esitken et al. (2010)
<i>Curcuma longa</i>	<i>B. megaterium</i>	Plant growth and yield	Sumathi et al. (2011)
<i>Momordica charantia</i>	<i>B. subtilis</i>	Enhanced yield, quality, root length, and dry root weight	Kumar et al. (2012a)
<i>Phyllanthus amarus</i>	<i>B. coagulans</i>	Improved growth, yield	Earanna (2001)
<i>Begonia malabarica</i>	<i>B. coagulans</i>	Biomass yield, nutrients, and secondary metabolites	Selvaraj et al. (2008)
<i>Mentha piperita</i>	<i>B. megaterium</i>	Root length, dry matter	Kaymak et al. (2008)
<i>Solanum viarum</i>	<i>B. coagulans</i>	P, Fe, Zn, Cu, and Mn content, secondary metabolites	Hemashenpagam and Selvaraj (2011)
<i>Sphaeranthus amaranthoides</i>	<i>B. subtilis</i>	Enhanced growth, biomass, nutrition	Sumithra and Selvaraj (2011)
<i>Withania somnifera</i>	<i>B. circulanse</i>	Increased plant height, root length, and alkaloid content	Rajasekar and Elango (2011)
<i>Rosmarinus officinalis</i>	<i>B. megaterium</i>	Increased oil content, yield in fresh herb, and total CHO	Abdullah et al. (2012)
	<i>B. circulanse</i>		

16.7 Future Prospect

The *Bacillus* species are a major integral component of soil microbial community and play an important role in the N fixation and phosphorus, potassium, zinc, and iron cycles in soil–plant rendering the plants available forms of nutrients. These bacterial strains have enormous potential for making use of fixed form of minerals and very slowly available nutrients under soil–plant systems with low availability in tropical and subtropical countries. The mechanism of mineral solubilization by *Bacillus* species has been studied in detail, but the K and Zn solubilization and Fe sequestration are a complex phenomenon affected by many factors, such as potential of bacterial strain used, nutritional status of soil, mineral type, amount of mineral, size of mineral particles, and environmental factors. Moreover, the sustainability of the *Bacillus* species after inoculation in soil as well as seed and seedling treatment is also important for mineral availability to benefit sustainable crop growth and development. Therefore, further study is needed to understand the problem of development of efficient and indigenous *Bacillus* species with microbial consortium for growth and yield of crops. Another big problem is the commercial propagation of soil microorganism's consortium and their preservation and transportation at farmer's fields for sustainable agricultural production.

16.8 Concluding Remarks

Climate change problems have raised great interest in eco-friendly sustainable agricultural management practices. The use of growth-promoting rhizobacteria is a promising solution for sustainable soil–plant–microbes, environmentally friendly agricultural production system. The studies on *Bacillus* species as plant growth-promoting activities in sustainable agriculture included isolating and screening antagonists targeting different diseases, evaluating their effectiveness in greenhouse as well as field, dissecting their mechanisms, and enhancing nutrient availability in agricultural soils. Research on improvement of *Bacillus* species through genetic engineering is also conducted in order to increase effectiveness under unfavorable conditions. *Bacillus* species control the damage to plants from phytopathogens and promote the plant growth by a number of different mechanisms and enhance the availability of nutrients for sustainable growth and development of agricultural production system.

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