Microbial Biofertilizer: A Potential Tool for Sustainable Agriculture

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Abstract

Surplus use of chemical fertilizers in crop field to meet the increasing demand of crop production has greatly hampered the soil ecosystem and human health. An alternative environment-friendly approach to sustainable agriculture is encouraging the use of biofertilizers. Plant growth-promoting microorganisms are one such group of potent biofertilizers. Many bacteria and fungi can develop close associations with the crop plant which improves growth, immunity and overall development of the plant. Thus understanding the action of various mechanisms exhibited by these microorganisms can show us the way to formulate the microbes to be used as biofertilizers. Continuous efforts are made to develop strategies for optimizing bioformulations. This chapter gives a deep understanding of the transformation of a microbe into a fertilizer. Distinctive properties of plant growth-promoting microbes and strategies to develop and optimize the bioformulations in addition to the phenomenon of integrated management have been discussed broadly.

Keywords

Fertilizer • Plant growth-promoting microorganisms • Biofertilizers • Bioformulation

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2.1 Introduction and Brief History on Microbial Biofertilizers

Agricultural practices always work with the aim of improving crop yield. For increasing productivity chemical fertilizers are being used. It leads to spoilage of the soil health through affecting its biodiversity by altering the chemical composition, microbial flora and ecosystem(s) (Wall et al. 2015). Early nineteenth-century chemical fertilizer industries started producing synthetic fertilizers and pesticides consisting of phosphorous (P), potassium (K) and nitrogen (N) to boost crop production and disease protection (Belay et al. 2002; Meng et al. 2013). Many researchers in recent years found the negative impact of chemical fertilizers and their hazardous nature on soil and human health. Farmers are being the target population for pesticide poisoning due to their direct exposure and lack of technical knowledge (Amundson et al. 2015). Current agricultural practices are quite dependent on synthetic chemical fertilizers as they directly help in increasing the required elements in soil. Studies suggest that long-term continuous application of chemicals results in soil acidification and reduced soil quality which ultimately hampers human health and creates environmental imbalance (Geisseler and Scow 2014). Hence there is an increasing need to have alternative sustainable agricultural practices and biotechnological approaches to increase crop productivity, improve soil health and conserve biodiversity. In this approach microbes play a vital role in maintaining agricultural sustainability by maintaining diversity of ecosystems and improving soil health in a safer way (McDaniel et al. 2014; Altieri 1999). Continuous interaction between the plant and its surrounding microbiome helps build some positive interactions. Depending upon the site of interaction, it is designated as phyllosphere, rhizosphere, epiphytic and endophytic bacteria (Rout 2014; Philippot et al. 2013; Lindow and Brandl 2003; Hartmann et al. 2009; Dong et al. 2003). Bacteria possessing the traits which benefit the plant in growth and disease protection are termed as plant growth-promoting bacteria (PGPB) (Mantelin and Touraine 2004; Bashan 1998; Bashan and de-Bashan 2005). Bioformulations were in agricultural practice in the history where discovery of Bassi in 1835 illustrated *Beauveria bassiana* infection in silkworm (Brownbridge et al. 2012). This discovery laid a path for identifying the role of microbes in disease protection. The discovery of Bt (*Bacillus thuringiensis*) toxin gave more strength to the idea of researchers to think more about microbes as an alternative for chemicals (Sayyed et al. 2003). Later most of the bacteria were reported for their plant growth-promoting and biocontrol activity. Many studies reported the successful application of various bioformulations in controlling the disease and improving plant growth (Glick and Bashan 1997). Beneficial microbes such as *Pseudomonas* spp. (Ahemad and Khan 2012a), *Bacillus* spp. (Canbolat et al. 2006), *Klebsiella* spp. (Ahemad and Khan 2011), *Rhizobium* (Ahemad and Khan 2009), *Azospirillum* (Rodrigues et al. 2008) and *Burkholderia* sp. (Guo et al. 2015) have been reported in different crops like rice (Mirza et al. 2006), green gram (Wani et al. 2007), wheat (Khalid et al. 2004), chickpea (Verma et al. 2014), maize (Braud et al. 2009a, b), black gram (Ganesan 2008), barley (Canbolat et al. 2006), *Brassica* (Belimov et al. 2005), soybeans (Gupta et al. 2005), sunflower (Faisal and

Hasnain 2005) and tomato (Ahemad and Kibret 2014). The commercialization of PGPR started in the late eighteenth century, and its popularity increased over the time with successful use as bioinoculants. The application of PGPB in sustainable agriculture is the need of the hour (Brockwell and Bottomley 1995; Vessey 2003). Mechanism of action of these microbial inoculants varies; researcher found that these are specific to host and region. Moreover, bacteria need to face unfavourable conditions after inoculation which make them reduce their expressive traits (Bashan 1998). Bacterial consortiums were made with multiple bacteria to combine multiple traits that benefit plant growth and combat against phytopathogens. Based on their expressive traits, numerous numbers of biofertilizers came into existence with various types of formulation. Moreover, recent development in studies on agriculture reveals that microbiome activities in soil and sustainable agriculture are interlinked to each other. This chapter will collectively focus on plant growth-promoting bacteria (PGPB) and their mechanism of action in growth promotion and role in bioformulations for sustainable development of agriculture.

2.2 Mechanisms of Action of Plant Growth-Promoting Rhizobacteria

2.2.1 Phosphate Solubilization

Phosphorus, a key nutritional element, plays an indispensable role in several plant developmental processes like macromolecular biosynthesis, photosynthesis, respiration, signal transduction and energy transfer (Khan et al. 2010). Despite the abundance of phosphorus in soil, sometimes it becomes inaccessible to plants, as they can only absorb soluble forms of phosphorus, i.e. mono- and dibasic phosphate (Jha et al. 2012). To resolve the problems related to plant phosphorus deficiency, chemically synthesized phosphate fertilizers are used. But the use of phosphate fertilizer comes with various drawbacks like release of highly volatile and poisonous hydrogen fluoride (HF) gas during manufacture (Sharma et al. 2013), heavy metal accumulation in soil and plant after application, eutrophication and hypoxia of lakes and marine estuaries (Lugtenberg et al. 2013), etc. Phosphate solubilizing microbes (PSM) provide an eco-friendly alternative to chemical fertilizers. The common mechanisms used by PSM for phosphate solubilization include (i) organic acid (acetic, malic, tartaric, gluconic, lactic, 2-ketogluconic, oxalic and succinic, citric) secretion (Patel et al. 2015) and (ii) extracellular enzyme (non-specific phosphatases, phytases, phosphatases and C-P lyases) production (Bloemberg and Lugtenberg 2001). Phosphate solubilization trait is widespread among rhizosphere microflora. Some of the efficient PSMs identified till date are *Aspergillus niger*, *Penicillium* sp., *Kluyvera cryocrescens, Pseudomonas aeruginosa, Bacillus amyloliquefaciens, Bacillus licheniformis, Bacillus atrophaeus, Paenibacillus macerans,* etc.

2.2.2 Nitrogen Fixation

Nitrogen (N) is the major mineral element required by plants for growth and development but is also the most limiting available nutrient for plant growth (Valentine et al. 2010). Dinitrogen constitutes a major portion of atmospheric gas (78%). However, most organisms cannot use this form of nitrogen. Prokaryotes are involved in the task of making dinitrogen available to other eukaryotes via the ATP-dependent process of biological nitrogen fixation (BNF) where dinitrogen is reduced to ammonia (Dos Santos et al. 2012). Bioavailability of nitrogen in the form of ammonia and nitrates is limited. Modern agriculture depends largely on nitrogen fertilizers for high crop yields (Galloway et al. 2008). The drawbacks of using chemical nitrogen fertilizers are:

(i) Production of nitrogen fertilizers requires a vast amount of non-renewable fossil fuel (Erisman et al. 2007).
(ii) High emission of greenhouse gases, which constitute a key factor in climate change.
(iii) Half of the nitrogen fertilizer applied is lost to leaching, resulting in significant health and environmental problems (Olivares et al. 2013).
(iv) Increase in soil acidity due to release of hydrogen ions in fertilizer applied on soil (Arma 2016).

Therefore, replacing chemical nitrogen fixation by BNF can generate a new perspective of agricultural sustainability (Farrar et al. 2014). Legumes fix atmospheric N through symbiotic nitrogen fixation (SNF). A part of the N fixed by legumes can be transferred to neighbouring non-fixing plants by means of N-transfer (Fustec et al. 2009). N-transfer is the movement of N from one legume plant (donor) to another nonlegume plant (receiver) in a mixed stand of plant community (Høgh-Jensen and Schjoerring 2000; Pirhofer-Walzl et al. 2012). N-transfer facilitates more efficient utilization of fixed N, minimizes N losses and maintains a good level of biomass production (Thilakarathna et al. 2016). *Paenibacillus polymyxa* P2b-2R, an endophytic strain, is capable of fixing nitrogen (N) and promoting growth in a broad range of hosts including canola (*Brassica napus* L.) (Anand et al. 2013; Padda et al. 2016). Recently it was reported that inoculation of maize and wheat with nitrogen-fixing rhizobacterium *Pseudomonas protegens* Pf-5 X940 largely improved nitrogen content and biomass accumulation in both vegetative and reproductive tissues, and this beneficial effect was positively associated with high nitrogen fixation rates in roots (Fox et al. 2016).

2.2.3 Phytohormone Production

Phytohormones produced by plant-associated microflora can stimulate plant growth and development by modulating endogenous plant hormone levels (Gray 2004) (Van Loon 2007). The most important microbial plant growth regulators reported till date include auxins such as indole-3-acetic acid, cytokinins and gibberellins (GAs). Eighty percent of rhizospheric microbes isolated from various crops are reported to produce auxin as secondary metabolites (Ahemad and Khan 2011). Plant-associated rhizobacteria can synthesize auxin in either L-tryptophan-dependent or L-tryptophan-independent pathways. Three tryptophan-dependent routes for auxin synthesis are known in rhizobacteria which are (i) indole-3-pyruvic acid (IPyA) pathway found in *Rhizobium, Bradyrhizobium* and *Azospirillum*; (ii) indole-3-acetamide (IAM) pathway used by some pathogenic bacteria like *Agrobacterium tumefaciens, Pseudomonas syringae, Pantoea agglomerans,* etc.; and (iii) tryptamine pathway found in *Bacillus licheniformis* and *Bacillus megaterium*. Rhizobacterial IAA has been identified as a key effector molecule in plant-microbe interaction causing either phytostimulation or pathogenesis (Ahemad and Khan 2012b; Mahanty et al. 2016). Besides IAA, there are reports of microbial phytostimulation by cytokinin production. *Bacillus megaterium* has been reported to enhance the growth of *Arabidopsis thaliana* and *Proteus vulgaris* seedlings via cytokinin synthesis (Castro et al. 2008). Bacteria belonging to diverse genera such as *Pseudomonas, Azospirillum, Bacillus, Proteus, Klebsiella, Xanthomonas, Pseudomonas,* etc. are well-characterized cytokinin producers. Apart from that gibberellin (GA) production has been detected in both bacteria and fungi. Though the exact role of bacterial GA is not known yet, GA-producing bacteria are still used for enhancing seed germination rate (Goswami et al. 2016).

2.2.4 Insecticidal Protein Production

Insect pests cause a major crop loss. Reduction of 39% yield and loss amounting US$ 500 million annually is caused by the fall armyworm *Spodoptera frugiperda* (Lepidoptera: Noctuidae) in corn (*Zea mays*) cultivation in Brazil. Native strains of entomopathogenic nematodes active against *S. frugiperda* represent a promising alternative to the intensive use of chemical insecticides to control fall armyworm population in corn plantations. Conventional control methods are ineffective especially when pest attacks the below-ground plant parts. Protecting plants with microbial agents such as PGPR is an ecologically friendly approach (Péchy-Tarr et al. 2013). Insecticidal toxins so far have been exploited mainly in two bacterial groups *Bacillus thuringiensis (Bt) and Photorhabdus/Xenorhabdus* species. *B. thuringiensis* is a gram-negative rod-shaped bacterium which produces a diverse range of insecticidal protein such as crystal (Cry) and cytolytic (Cyt) toxins (Roh et al. 2007). *Photorhabdus/Xenorhabdus* species are gram-negative bacteria producing insecticidal toxins (Tc) and live in symbiotic relationship with entomopathogenic nematodes (ffrench-Constant et al. 2007). Two related strains of *P. fluorescens* CHA0 and Pf-5 exhibit both antifungal activity and insecticidal activity. Their insecticidal activity depends greatly on a large protein production termed as the Fit toxin (Péchy-Tarr et al. 2013) which also contributes to oral insecticidal activity (Ruffner et al. 2013). *Yersinia entomophaga* MH96 secretes Yen-Tc protein toxin complex which when ingested by sensitive insects causes its death within 72 h of infection (Busby et al. 2012). Insecticidal toxin (Tc) formed by three-component (TcA-, TcB- and TcC-like proteins) complexes were found effective for symbiosis and insecticidal activity (ffrench-Constant et al. 2007). Symbiotic bacterial interactions with nematodes is one of the viable alternative for chemicals as their interaction leads bacteria to produce factors that can control/kill the insect host and facilitate the growth of nematodes. Bacterial ureases have been studied extensively for their role in insecticidal activity (Salvadori et al. 2012).

2.2.5 Antibiotic Production

Indirect mechanism of plant growth promotion by bacteria involves antibiotic production as well which have inhibitory effects on pathogenic organisms in the rhizosphere (Glick 1995) (Ahmad et al. 2008). Antibiotics constitute a wide and heterogeneous group of low molecular weight chemical organic compounds that are produced by a wide variety of microorganisms (Raaijmakers et al. 2002). The basis of antibiosis relies on the secretion of molecules which can reduce or kill the growth of target pathogen (Glick et al. 2007). Some antibiotic compounds are diffusible such as phenazines, phloroglucinols, pyoluteorin, pyrrolnitrin and cyclic lipopeptides, and some are volatile like hydrogen cyanide (HCN) (Haas and Défago 2005). Mostly the *Pseudomonas* genus in comparison to other bacterial species has the ability to produce antibiotics (Santoyo et al. 2012). Pyoluteorin (Plt), phenazine-1-carboxylic acid (PCA), 2,4-diacetylphloroglucinol (DAPG), pyrrolnitrin (Prn), hydrogen cyanide (HCN) and pyoluteorin (Plt) and protein-type (bacteriocins) are some types of antimicrobial compounds synthesized by *Pseudomonas* (Haas and Keel 2003). 2,4-DAPG is the most efficient antibiotic in the control of plant pathogens and can be produced by various strains of *Pseudomonas* (Nakkeeran et al. 2006). This antibiotic has antifungal, antibacterial and antihelmintic properties (Loper and Gross 2007; Velusamy et al. 2006; Cronin et al. 1997). Thomashow and Weller (1988) demonstrated the first experimental proof that a *Pseudomonas* antibiotic can suppress plant disease in an ecosystem. *Pseudomonas fluorescens 2–79* strain (isolated from the rhizosphere of wheat) synthesized phenazine antibiotic phenazine-1-carboxylic acid (PCA) which could suppress take-all disease caused by the fungal pathogen *Gaeumannomyces graminis* var. *tritici* (Ggt) on wheat. *Pseudomonas* PCA-negative mutants are partially devoid of their ability to inhibit the fungus in vitro and to suppress take-all disease in vivo.

Recently, *Pseudomonas* and *Bacillus* species are known to have a new class of biocontrol agent called lipopeptide (LP) bio-surfactants which possess positive effect on competitive interactions with organisms such as bacteria, fungi, nematodes and plants (De Bruijn et al. 2007; Raaijmakers et al. 2010). *Bacillus* LPs were mostly studied as antagonists, but they also facilitate root colonization (Bais et al. 2004). Khabbaz et al. (2015) reported that *Pseudomonas fluorescens* Pf 9A-14, *Pseudomonas* sp. Psp. 8D-45 and *Bacillus subtilis* Bs 8B-1 showed broad-spectrum antagonistic activity and provided suppression of *Pythium* damping-off and root rot of cucumber. *Pseudomonas* strains contained genes for biosynthesis of antibiotics, viz. PCA, 2, 4-diacetylphloroglucinol, pyrrolnitrin and pyoluteorin, whilst *B. subtilis* Bs 8B-1 contained antibiotic lipopeptides such as fengycin, bacillomycin, bacilysin, surfactin and iturin A. These antagonistic bacteria have also shown a significant increase in fresh weights of both cucumber and radish plants. The antagonistic activity of the three bacterial strains and the growth inhibition of *Phytophthora capsici* and *Rhizoctonia solani* might have been due to the production of different types of antibiotics.

2.2.6 Siderophore Production

Along with antibiotics, siderophores also function in root disease suppression (Martínez-Viveros et al. 2010). The term “siderophores” is derived from the Greek word meaning “iron carriers”. They are relatively low molecular weight, ferric ion-specific chelating agents produced and utilized by bacteria and fungi growing under low iron stress (Neilands 1995). The primary function of these compounds is to scavenge the ferric iron [Fe (III)] from different terrestrial and aquatic habitats and thereby make it available for microbial and plant cells for their cellular growth and metabolism (Ahmed and Holmström 2014). The importance of iron (Fe) in the growth of almost all living organisms is because it acts as a catalyst in enzymatic processes, oxygen metabolism, electron transfer and DNA and RNA syntheses (Aguado-Santacruz et al. 2012). Acquirement of Fe through siderophore production displays the competitive fitness of plant growth-promoting bacteria to colonize plant roots (Barton and Abadia 2006) thereby outcompeting the pathogenic microorganisms in the rhizosphere (Siddiqui 2006). The primary role of siderophore is to sequester iron, but it also forms complexes with other essential elements, viz. Mo, Mn, Co and Ni, in the environment and make them available for microbial cells (Bellenger et al. 2008) (Braud et al. 2009a, b). pH influences Fe(III)-siderophore complex formation. Fe has to compete against free proton for siderophore binding sites and also against metals such as divalent cations (Cd2+, Cu2+, Ni2+, Pb2+ and Zn2+) (Albrecht-Gary and Crumbliss 1998), trivalent cations (Mn3+, Co3+ and Al3+) and actinides (Th4+,U4+ and Pu4+) (Weber 2005).

2.2.7 Hydrogen Cyanide Production

Many rhizobacteria are capable of producing a volatile compound known as HCN which plays a role in biocontrol of certain plant pathogens (Martínez-Viveros et al. 2010) (Gupta et al. 2015). HCN genes are widely distributed among many *Pseudomonas* strains producing antibiotic 2,4-DAPG (Haas and Défago 2005). The *hcnAB* genes are shown to be particular in detecting HCN-producing pseudomonas among the bulk isolates (Svercel et al. 2007). In addition with the established hypothesis of biocontrol by HCN-producing strains, another new hypothesis evolved where it is stated that HCN is involved in geochemical processes and regulation of nutrient availability. HCN is also involved in metal sequestration (Wongfun et al. 2013), and this sequestration leads to increased availability of phosphate (Rijavec and Lapanje 2016).

2.2.8 Bacterial Volatile Compounds

Many PGPRs have been reported to secrete volatile compounds known as bacterial volatile compounds (BVCs) which trigger plant growth and immunity (Chung et al. 2016). For a rhizobacteria to contribute in plant's growth promotion, it is studied that there must be a close association between the microbe and the root, but volatile compound-producing rhizobacteria does not require any established physical contact to trigger growth response (Ortíz-Castro et al. 2009). BVC are low molecular weight compounds (<300 Da) secreted by bacteria (Chung et al. 2016). Bacterial volatiles include inorganic compounds such as ammonia, H2S, HCN and NO, and therefore these volatiles are referred to as BVCs rather than volatile organic compounds (VOCs) (Audrain et al. 2015). BVCs such as 2,3-butanediol and acetoin accelerate plant growth and induce systemic resistance (Ryu et al. 2003). Bacteria-emitting BVC was reported to colonize the maize tissue both underground and aboveground and secrete BVC which strikes the plant's physiology, growth and defence (D'Alessandro et al. 2014). *Bacillus* sp. B55 secretes sulphur-containing BVC-dimethyl disulphide (DMDS) which increased sulphur content in *Nicotiana attenuata* and also enhanced the plant growth (Meldau et al. 2013).

2.2.9 Rhizoremediation

Microbes have the potential to detoxify various soil contaminants (petroleum hydrocarbons (PHCs), pesticides halogenated hydrocarbons, polycyclic aromatic hydrocarbons (PAHs), heavy metals, etc.) through diverse mechanisms like bioexclusion, biosorption, bioleaching and bioaccumulation. Degradation of contaminants occurs in the rhizosphere by combined action of microbial products and plant root exudates. Bioremediation of non-biodegradable heavy metals has been reported to be done by different plant beneficial rhizobacteria like *Achromobacter xylosoxidans, Azotobacter chroococcum, Ochrobactrum* sp.*, Bacillus subtilis, Bacillus megaterium, Bradyrhizobium, Pseudomonas sp., Mesorhizobium, Brevibacillus* sp., *Kluyvera ascorbata, Pseudomonas putida, Ralstonia metallidurans, Rhizobium, Sinorhizobium* sp.*, Pseudomonas aeruginosa, Variovorax paradoxus, Psychrobacter* sp.*, Xanthomonas* sp., etc. (Mahanty et al. 2016). Microbes can do either biotransformation or biodegradation to detoxify the pesticides. For microbial biodegradation, enzyme systems involved are hydrolases, esterases and the mixed function oxidases (MFO) in the first metabolic stage and the glutathione S transferases (GST) system in the second phase (Ortiz-Hernández et al. 2013). It has been reported that *Azospirillum, Enterobacter, Azotobacter, Bacillus, Klebsiella, Gordonia, Paenibacillus, Serratia, Pseudomonas*, etc. can reduce pesticide toxicity in soil (Shaheen and Sundari 2013).

2.2.10 Induced Systemic Resistance

Defence responses in plants can be activated via two mechanisms. One is induced systemic resistance (ISR) triggered by nonpathogenic PGPR, and the other is systemic acquired resistance (SAR) triggered by a pathogenic agent (Pieterse et al. 2009). SAR leads to activation of pathogenesis- related (*PR*) genes and involves salicylic acid (SA) as signalling molecule (Durrant and Dong 2004). ISR is SA independent but requires signalling pathway of jasmonic acid (JA) followed by ethylene signalling (van Loon et al. 1998). Yet both ISR and SAR require nonpathogenesis-related protein (NPR1), a key regulatory protein. ISR prepares the plant to encounter pathogen by priming for enhanced defence. During pathogen or insect attack, the defence response is accelerated leading to faster and enhanced resistance (Conrath et al. 2006). SAR and ISR pathways have been reported to exert additive effect on *A. thaliana* against a broad range of pathogens (van Wees et al. 2000). The enhanced defence response due to the additive effect was supported by molecular studies which revealed an increased expression of pepper defence genes *CaTin1*, *CaPR1* and *CaPR4* after application of combined treatment of *Bacillus pumilus* INR7 with a chemical inducer, benzothiadiazole (BTH), in the field and subsequent suppression against bacterial spot disease caused by *Xanthomonas axonopodis* pv. vesicatoria in pepper (Yi et al. 2013).

2.2.11 Induced Systemic Tolerance

Induction of microbe-driven abiotic stress tolerance in plant is referred to as "induced systemic tolerance (IST)" (Yang et al. 2009). Molecular mechanism of plant-microbe crosstalk associated with IST is largely unknown. Beneficial microbes can enhance survivability of stress-affected plants by diverse mechanisms. One of the most important mechanisms is the modulation of hormonal status in host plant. In response to stress stimuli (salinity, drought, metal toxicity, etc.), retardation in plant growth and development is due to the increase in stress ethylene level. Some plant growth-promoting bacteria produce ACC deaminase enzyme which cleaves ACC, the precursor of ethylene to ammonia and α-ketobutyrate (KB), thereby lowering ethylene level and promoting plant growth under stress. The level of ACC deaminase activity differs among bacterial genera under various environmental conditions (Singh and Jha 2016). Experimental evidence suggests that bacteria showing ACC deaminase activity approximately >20 nmol α-ketobutyrate (KB) mg-1 h-1 are sufficient to reduce the growth inhibitory effects of stressors (Penrose and Glick 2003). Volatile emission is another important microbial trait involved in plant growth stimulation under stress (Ryu et al. 2003). For instance, VOC produced by *Bacillus subtilis* confers salt tolerance in *Arabidopsis thaliana* by modulating the expression of high-affinity Na+ transporter HKT1 in a tissue-specific manner (Zhang et al. 2008).

Table 2.1 List of some beneficial plant growth-promoting traits

Trait	Role	Microbe	Reference
Phosphate solubilization	1. Organic acid production	*Bacillus licheniformis*; *B. amyloliquefaciens*; *Penicillium sp.*	Chen et al. (2006) and Wakelin et al. (2004)
	2.Phytase production	*Bacillus mucilaginosus; Aspergillus niger*	Li et al. (2007) and Vassilev et al. (2007)
	3. Phosphatase production	*Burkholderia cepacia, Serratia marcescens*	Ryu et al. (2005) and Unno et al. (2005)
Nitrogen fixation	1. Symbiotic	*Rhizobium phaseoli; Vesicular-arbuscular mycorrhizal fungi*	Shah et al. (2010)
	2. Non-symbiotic	*Gluconacetobacter diazotrophicus*	Bhattacharyya and Jha (2012)
Phytohormone production	1. IAA production	*Bacillus licheniformis; Phoma glomerata* and *Penicillium* sp.	Goswami et al. (2016) and Waqas et al. (2012)
	2. Cytokinin production	*Bacillus megaterium*	Castro et al. (2008)
	3. Gibberellin production	*Acetobacter diazotrophicus, Phoma glomerata* and *Penicillium* sp.	Basti et al. (1998) and Waqas et al. (2012)
Biocontrol	1. Extracellular enzyme production		
	(a) Chitinase	*Enterobacter agglomerans*	Nielsen and Sörensen (1999)
	(b) Glucanase	*Bacillus cepacia*	Compant et al. (2005)
	2. Antibiotic production	*Pseudomonas fluorescens; Trichoderma koningii*	Thomashow and Weller (1988) and Xiao-Yan et al. (2006)
	3. Siderophore production	*Pseudomonas aeruginosa*	Braud et al. (2009a, b)
	4. HCN production	*Pseudomonas chlororaphis*	Nandi et al. (2015)
Potassium solubilization	Production and excretion of organic acid and inorganic acid	*Bacillus mucilaginosus*	Ullman et al. (1996)
Induced systemic tolerance	1. ACC deaminase production	*Achromobacter piechaudii; Trichoderma asperellum; Penicillium citrinum*	Mayak et al. (2004), Viterbo et al. (2010) and Jia et al. (2000)
	2. Exopolysaccharide production	*Oceanobacillus profundus*	Qurashi and Sabri (2011)
	3. VOC production	*Bacillus amyloliquefaciens*	Choi et al. (2014)

2.3 Strategies for Development and Optimization of Bioformulations

2.3.1 Large-Scale Production of Strains

For mass production of inoculants, the viable cells of the strains have to prove efficient enough in maintaining their genetic stability, exerting the desired effect on target crops and their survival under adverse conditions. Preparation of microbial inoculum is considered to be key factor in maintaining viability of the inoculant on seed (Moënne-Loccoz et al. 1999). The production of microbial inoculants starts with preparation of broth culture to reach high population density of bacterial cells. The main factors during inoculum preparation include (i) the specified growth media; (ii) optimal growth conditions such as pH, temperature, O2, etc.; (iii) purity of the media; and (iv) cost (Herrmann and Lesueur 2013). The microbial cultures are then inoculated on different types of carrier which serves as the delivery vehicle of live biofertilizers from the factory to the field (Bashan et al. 2014). Acclimatization of inoculants in the carrier material for several days prior to application to seed can improve the inoculums' efficacy (O'Callaghan 2016).

2.3.2 Formulation

Jones and Burges (1998) regarded formulation as vital factor in bioinoculant development. Roles of formulation are to (i) stabilize the microbe, (ii) help in the delivery of the microbe to the target zone, (iii) protect the microbe during seed storage and (iv) enhance the functionality of the microbe in situ after planting. Over the years scientists have been trying to improve the survival of pre-inoculated seeds, and so various formulation efforts are being targeted. Microbial formulations are divided into conventional type and advanced type. Conventional type includes (1) **solid formulation** (peat, granules, powders, etc.), but microbial shelf life is less in it due to desiccation and (2) **liquid formulation**, based on broth cultures, but they lack carrier protection and quickly lose viability on the seed. Advanced type involves the most promising technique for constructing carriers of microorganisms called (1) **microencapsulation** formulation which has been proven to be advantageous over conventional types (John et al. 2011). Biofilms have been proposed as possible bioformulation for both bacteria and fungi (Seneviratne et al. 2008). Recently it was reported that *Trichoderma atroviride* spores can be formulated by an adhesive, xanthan gum, provided optimal storage conditions are maintained and thus can be effectively delivered on to seeds (Swaminathan et al. 2016).

2.3.3 Storage and Transport

Formulation is important during storage and transport of the biofertilizers (Malusá et al. 2012). Thus endurance of bioinoculant is necessary during its storage period and also after its application onto the soil where it has to compete with other native microbes for space and nutrient (Bashan et al. 1995). The carriers and optimum conditions required to maintain the bioinoculants differs as it depends on the strains used. PGPR continued to multiply and maintain their metabolic activity when peat was used as carrier (Rice et al. 2000). The sludge-based carrier could maintain rhizobia population at neutral pH and water holding capacity even after 130 days of storage at 25 ° C (Ben Rebah et al. 2002). Encapsulation of microbial cells offers longer viability when stored at 4 ° C. Moreover encapsulated bacteria could be stored at 4 °C or room temperature for up to 6 months with static population size (Rouissi et al. 2010). Long-term storage of bioinoculants results in cell sedimentation. Vandergheynst et al. (2007) used hydrophobic silica nanoparticles for thickening the oil phase which greatly cut down cell sedimentation thereby improving cell viability during storage. The reason behind is the dispersed water retaining the oil which prevented cells from desiccation. More insights into overcoming the problem of cell sedimentation using nanomaterials will be beneficial for further long-term storage of biofertilizers.

2.3.4 Inoculation in the Field

Introduction of the biofertilizers into the field depends on various factors including concentration of the inoculums, mode of biofertilizer application, competition of inoculants with the native niche for survival and user-friendliness of the bioinoculant (Dey et al. 2012). Farmers need to have proper knowledge about how microbes perform in soil prior to their inoculation in the fields (Date 2001). The lower quantity of inoculants having high cell concentration (10^4–10^6) shows similar efficiency as the higher quantity of inoculants with lesser cell concentration does (Schulz et al. 2008). Mode of biofertilizer application is mainly done by four ways: (a) inoculation of seeds with powder formulation, (b) water-suspended peat sprayed onto furrow during seed sowing, (c) soil inoculation with peat granules and (d) liquid formulations (Bashan 1998). Biofilm-based application of microbial consortium was proved to be advantageous for fixing N_2 in the soybean over the conventional practise of rhizobia inoculation (Jayasinghearachchi and Seneviratne 2004). Since the microbial population in the soil could get diluted along with time, repeated application of bioinoculum during the growing season is required to escalate the effect of microbial application (Bashan et al. 1995) (Malusá et al. 2012). Agrichemicals are often used as seed dressing. Thus compatibility of seed inoculants with those agrichemicals such as pesticides is the most important because pesticides have been reported to alter the structure and function of the bioinoculum (Fox et al. 2007; O'Callaghan 2016).

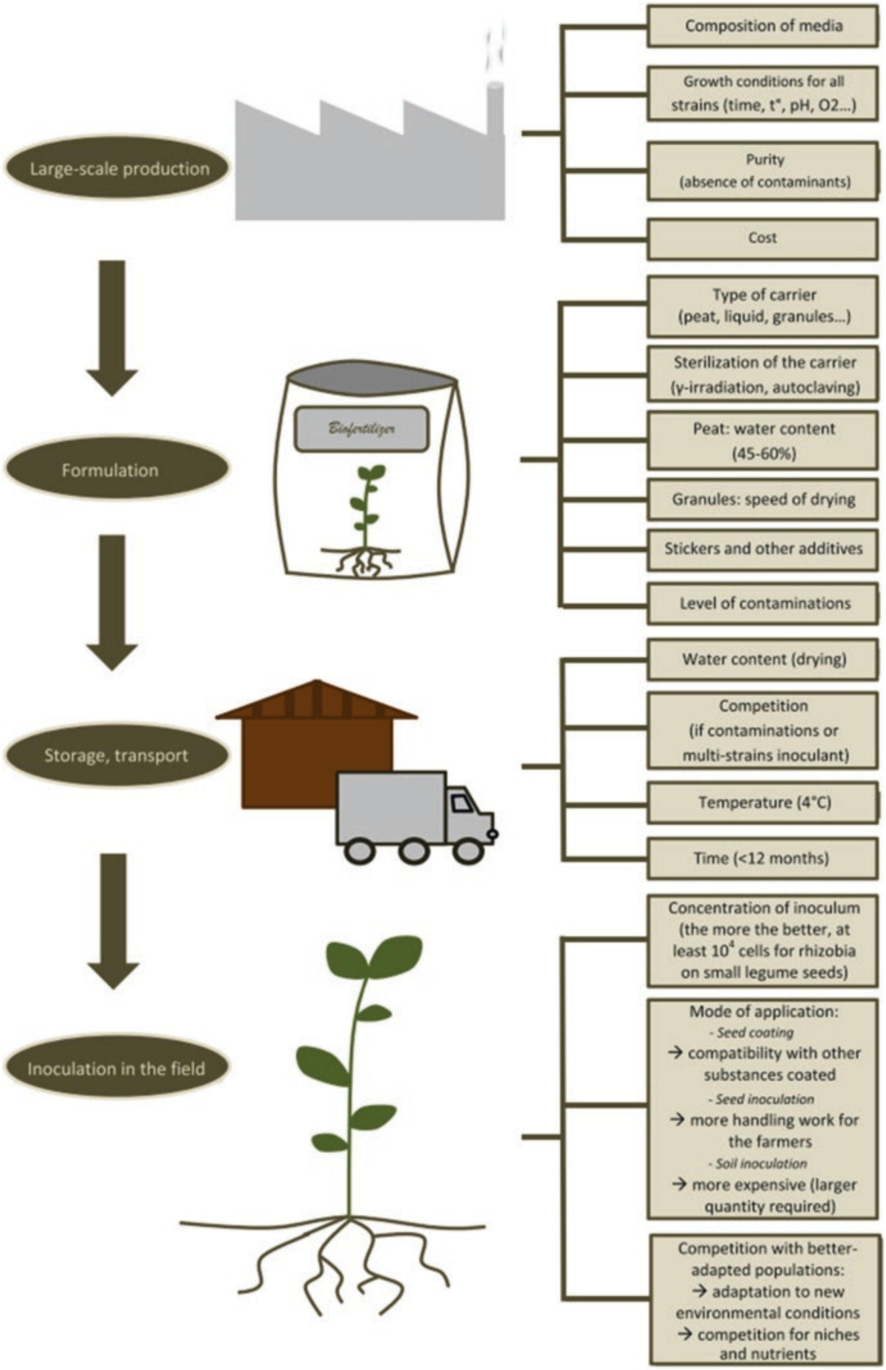

Fig. 2.1 Steps involved in inoculum preparation to inoculation in field (Herrmann and Lesueur 2013)

2.3.5 Integrated Management

Crop production is at stake due to increase in incidences of pests, namely, animal pests (insects, nematodes, mites, etc.), plant pathogen (bacteria, protozoa, fungi, virus) and weeds. Crop protection is being developed for prevention and control of pests (Oerke 2006). Integrated crop protection management can be broadly classified into four types: (i) integrated soil fertility management (ISFM) (ii) integrated pest management (IPM), (iii) integrated weed management (IWM) and (iv) integrated nutrient management (INM). However on a broader perspective, it is seen that all the four kinds are interrelated.

Soil infertility is the considered to be greatest obstacle for increasing crop yield in developing nations worldwide. For farmers to get benefited by the application of modernized tools in farming, soil fertility has to be restored (Khosro and Yousef 2012). Physical, chemical and biological properties of soil also influence the crop plant's ability to resist or tolerate insect pests. A fertile soil possesses high organic matter and beneficial organisms which fight infection and provide nutritional balance to the plant. Imbalanced nutrition in soil can reduce pest resistance (Altieri and Nicholls 2003) (Magdoff and van Es 2000). The soil microbes can thus be involved in integrated pest management programmes (Gadhave et al. 2016). The techniques used by farmers for pest management are also applicable for soil fertility management and vice versa (Altieri and Nicholls 2003).

Pests contribute to huge amount of crop loss (Oerke 2006). FAO regards IPM as a pillar of both sustainable intensification of crop production and pesticide risk reduction (http://www.fao.org/agriculture/crops/thematic-sitemap/theme/pests/ipm/en/) since it promotes biological activity in soil, minimizing the use of pesticides by incorporating alternative methods to control pests (Hobbs et al. 2008).

Among pests, weeds are also considered as major biotic constrain to food production (Rigby and Cáceres 2001). Integrated weed management system follows cultural practices, viz. crop rotation, irrigation, sowing, intercropping, etc., to reduce weed emergence (Barberi 2002). Biofertilizer like *Azolla* forms a thick mat of thallus on standing water surface in the lowland rice farming system preventing light to penetrate the weed seeds resulting in weed suppression (Kathiresan 2002). Insect pests are also welcomed by many weed species and so indirectly IWM also exerts positive influence on IPM (Kathiresan 2007).

INM aims to subside the harmful impact of chemical fertilizers containing elements like N, P, K, etc. (Adesemoye and Kloepper 2009) by development of microbial inoculants consisting of nitrogen fixing, phosphorus dissolving and potassium mobilizing organisms (Sangeetha and Suseela Bhai 2016). Adesemoye et al. (2008) showed that plant N content was increased after inoculation with PGPR which might have resulted from increased fertilizer N utilization efficiency in an INM system. Co-inoculation of wheat plant with *Azospirillum* and P-solubilizing bacteria increased N and P uptake by the plant (El-Komy 2005).

A deep insight into understanding the interaction among microbe-fertilizer-plant can help in developing new strategies for integrated management. This will focus on improving the agricultural practices by lowering the adverse effects exerted on the environment due to the use of conventional agriculture practices (Geisseler and Scow 2014). Microbial fertilizers are promising than the conventional chemical fertilizers since they do not possess threat to the ecosystem in the long run.

2.3.6 Commercialization

Key for extensive commercialization of bioinoculants demands coordination between the research and industrial sector and insightfulness of the farmers (Glick 2012). Steps involved in successful commercialization are as follows:

1. Expressive biological functional traits of bacteria should be well determined.
2. Indigenous varieties should be engineered for appropriate environmental conditions.
3. Better evaluated understanding on rhizosphere, phyllosphere, endophytic microbes interactions and their beneficial and harmful effects.
4. Inter- and intramicrobial communication studies on healthy biodiversity (plant-fungi, bacteria-fungi, bacteria-insects, bacteria-bacteria) for welfare of the plant.
5. Farmer friendly methods of application development.

2.4 Mechanism of Biofertilizer Action on Plant

Depending upon the mechanism of action, present-day microbial biofertilizers can be broadly divided into two categories, viz. nutrient uptake stimulators and biopesticides. The fate of the designed bioformulation and its performance under field condition largely depends upon the properties of microbe(s) by which it is made of. Various microbes can promote plant growth either directly or indirectly by diverse mechanisms. Depending upon the microbial functional trait, bioformulations are classified into three major groups: nitrogen fixers, phosphate solubilizers and plant growth-promoting microbes (PGPM).

Nitrogen-fixing microorganisms convert atmospheric dinitrogen into plant-usable form as ammonia by an ATP-driven process called biological nitrogen fixation (BNF) (Gothwal et al. 2008). Biological nitrogen fixers can be free-living, associative or symbiotic in nature (Mazid and Khan 2014). As specific nitrogen fixers can only colonize certain plant groups, so depending upon that, the specific bioformulation for a plant is recommended. For example, bioformulations containing symbiotic nitrogen fixer, *Rhizobium* is appropriate for leguminous plants. Similarly, *Azospirillum,* a free-living nitrogen fixer, is particularly applied to C4 plants, because it is dependent on the salt of organic acids like malic and aspartic acid for nitrogen fixation (Mazid and Khan 2014).

The key enzyme complex required for biological nitrogen fixation is nitrogenase encoded by the nif gene cluster (Goswami et al. 2016). Nitrogenase complex is made up of two components, viz. dinitrogenase reductase (iron protein) and dinitrogenase (molybdenum – iron protein). Dinitrogenase component is responsible for fixing nitrogen by using the electrons provided by dinitrogenase reductase (Mahanty et al. 2016).

In case of legume-*Rhizobia* (*Rhizobium*/*Bradyrhizobium*/*Sinorhizobium*/*Azorhizobium*/*Mesorhizobium*) association, (iso)flavonoids present in plant root exudate act as stimuli for the activation of nodulation genes (nod, nol, noe) of compatible rhizobia and subsequent production of nodulation factor (lipochitin oligosaccharides) to initiate root curling followed by nodulation of leguminous plant (Ibáñez et al. 2015). Research studies reported that plant ethylene level increases upon *Rhizobium* infection in order to prevent subsequent rhizobial infection and promote nodulation (Abeles et al. 1992; Mahanty et al. 2016). It has been found that some rhizobial strains increase nodule number by producing a phytotoxin called rhizobitoxine which inhibits ACC synthase enzyme in legumes and thereby lowers plant ethylene level (Vijayan et al. 2013).

Another important group of microbial biofertilizers called phosphate solubilizing microbes can solubilize bound phosphorus from organic or inorganic complexes and make it available for plant uptake. Low molecular weight inorganic acids (such as gluconic and citric acids) produced by soil bacteria possess carboxyl and hydroxyl groups which can chelate the cations (calcium, aluminium, iron) bound to insoluble phosphatic compounds accompanying the release of plant-usable soluble phosphorus. *Rhizobium leguminosarum*, *Rhizobium meliloti* and *Bacillus firmus* have been reported to produce 2-ketogluconic acid for mineral phosphate solubilization (Abd-Alla 1994; Sridevi and Mallaiah 2009). Microbes can also mineralize complex structured organic phosphorus (tricalcium phosphate, rock phosphate, aluminium phosphate, etc.) by secreting a range of enzymes like non-specific phosphatases which catalyse the hydrolysis of phosphoric esters and convert organic phosphorus to inorganic form, phosphatases and C-P lyases that break C-P bonds in organophosphonates and phytases for phosphorus release from phytic acid (Goswami et al. 2016). It has been found that some microbes can perform both solubilization and mineralization activity (Pereira and Castro 2014) proving them extremely efficient biofertilizing agent.

Besides nitrogen fixation and phosphate solubilization, other prominent microbial traits involved in plant growth enhancement include phytohormone production, siderophore production, antibiotic production, HCN production and ACC deaminase production. Phytohormone-producing bacteria are ubiquitous in plant rhizosphere and serve as a potent candidate for biofertilizer formulation due to its ability of regulating plant growth by modulating endogenous hormonal level in plants. *Agrobacterium tumefaciens*, *Bacillus megaterium, Pseudomonas syringae*, *Pantoea agglomerans*, *Rhizobium*, *Bradyrhizobium*, *Erwinia herbicola,* etc. are reported to enhance plant growth by IAA production (Goswami et al. 2016).

Bacterial siderophore production is involved in improving plant iron nutrition. Iron predominantly exists in soil as Fe^{3+} which easily forms insoluble oxides and hydroxides inaccessible for assimilation in both plant and bacteria. Siderophore, a low molecular weight compound (usually <1 KDa), produced by bacteria and fungi under iron-limiting condition binds with Fe^{3+} ion and reduces it to Fe^{2+} molecule.

Release of Fe^{2+} molecules in rhizosphere by microbes benefits plants in terms of iron utilization (Mahanty et al. 2016).

Occurrence of ACC deaminase production trait in bacteria is directly linked to induced systemic tolerance (IST). Under stressful condition, plant ethylene level increases. 1-aminocyclopropane-1-carboxylic acid (ACC) is the precursor of ethylene. ACC deaminase produced by bacteria cleaves ACC into α-ketobutyrate and ammonia, thereby reducing plant ethylene level, so that plant can grow well under unfavourable condition. Scientific studies suggested that ACC deaminase-producing bacterial strains like *Achromobacter piechaudii* ARV8, *Pseudomonas fluorescens*YsS6, *Pseudomonas migulae* 8R6, etc. can reduce adverse effect of different stress conditions (drought, salinity, flooding, temperature, heavy metal toxicity, etc.) on plant growth and yield (Ali et al. 2012; Glick 2014; Mayak et al. 2004; Goswami et al. 2016). *Pseudomonas putida* Rs-198 confer salt tolerance in cotton by decreasing Na^{+} absorption and increasing the rate of uptake of other divalent cations like K^{+}, Mg^{2+} and Ca^{2+}(Yao et al. 2010).

Another promising strategy of microbial plant growth promotion is the biocontrol. Biocontrol can be achieved by beneficial microbes by production of various anti-phytopathogenic metabolites, viz. HCN, 2,4 diacetylphloroglucinol (DAPG), phenazine-1-carboxylic acid (PCA), phenazine-1-carboxamide (PCN), pyoluteorin (Plt), pyrrolnitrin (Prn), oomycin A, viscosinamide, butyrolactones, kanosamine, zwittermicin A, aerugine, rhamnolipids, cepaciamide A, ecomycins, pseudomonic acid, azomycin, antitumor antibiotics FR901463, cepafungins and antibiotic karalicin (Bhattacharyya and Jha 2012). It was reported that soil inoculation with *Pseudomonas fluorescens* and arbuscular mycorrhizal fungi can prevent root rot disease in *Phaseolus vulgaris* L (Neeraj and Singh 2011; Bhardwaj et al. 2014). Mycorrhiza produces bioactive compounds called Myc factors which are perceived by host roots for activation of symbiosis (SYM) pathway (Bhardwaj et al. 2014).

It was observed that some biofertilizers like *R. leguminosarum*, *Rhizobium sp*. IRBG 74 and Bradyrhizobium sp. IRBG 271 can increase net photosynthetic rate of plants (Mahanty et al. 2016). PGPR Strains like *Achromobacter xylosoxidans*, *Azotobacter chroococcum*, *Bacillus subtilis*, *Bradyrhizobium*, *Pseudomonas* sp., *Brevibacillus* sp., *Kluyvera ascorbata*, Mesorhizobium, etc. were reported to possess bioremediation potential (Shinwari et al. 2015; Mahanty et al. 2016). Biofertilizers with bioremediation potential may play pivotal role in restoring fertility of contaminated unfertile soil.

2.5 Commercially Available Bioformulations: Success and Drawback

In the present era marked by global warming and food scarcity, biofertilizers have arisen as a promising substitute to hazardous agrochemicals. Problems arising due to the use of various chemical fertilizers in modern agricultural practices are innumerable and increasing day by day. It has been reported that chemical fertilizers cause mineral imbalance in plant body resulting in the reduction of valuable nutrients in food. For example, excess of potassium treatment in plant can decrease ascorbic acid and carotene in foods. Moreover, methemoglobinemia may arise due to consumption of vegetables grown in NO_3 rich soil (Mazid and Khan 2014). On the contrary, biofertilizers can perform all functions of agrochemicals like soil enrichment, plant growth stimulation, yield enhancement, etc. without causing any deleterious effect to the ecosystem.

Rhizobium, belonging to the family *Rhizobiaceae*, is a potent biofertilizer able to fix atmospheric nitrogen by forming symbiotic relation with legumes (lentil, pea, black gram, soybean, ground nut, etc.) and certain nonlegumes (*Parasponia*) (Saikia et al. 2007; Mazid and Khan 2014). Some crop-specific inoculants of *Rhizobium* include *Rhizobium japonicum* for soybean, *R. trifolii* for berseem, *R. lupini* for chickpea, *R. phaseoli* for green gram and *R. Meliloti* for lucerne. Though rhizobium is a very good substitute of nitrogen fertilizers, its application is limited by crop specificity and variable response under field condition. Another important nitrogen-fixing biofertilizer, *Azotobacter,* can fix nitrogen non-symbiotically. Problem associated with *Azotobacter* application is that it requires a large amount of organic C and Mo for stimulating nitrogenase enzyme activity during N fixation (Khan et al. 2011; Mazid et al. 2011). For optimizing biofertilizer activity, we should first know the constraints. Major constrains related to application of biofertilizer in agricultural system include (Table 2.2):

- Limited resource generation
- Problems in quality control
- Problems with inoculation techniques
- Compatibility with host genotype
- Standardization of proper dosage
- Occurrence of mutation in microbial strain throughout the bioformulation development
- Lack of assurance about the biofertilizer activity under various climatic conditions
- Impact of season change on biofertilizer activity
- Influence of native soil microflora
- Wrong inoculation techniques
- Unavailability of suitable carrier resource
- Lack of awareness among farmers
- Market level constraints
- Inadequate experienced staff

2.6 Conclusion and Future Perspective

Major constraint for biofertilizers is that their effect in field and lab conditions varies. Commercialization of biofertilizers is lacking a regulatory body. Policy making authorities should make guidelines in preparation of biofertilizer and its activity to be accepted globally. Farmer-friendly approaches with novel techniques of

Table 2.2 List of some commercially available microbial biofertilizers

Commercial bioformulation	Microbial ingredient(s)	Benefits	Reference
BiotaMax	*Bacillus subtilis, B. megaterium, B. licheniformis, B. pumilus, B. laterosporus, Paenibacillus polymyxa, Trichoderma harzianum, T. viride, T. polysporum, T. koningii*	Increases root mass – stronger, healthier root systems	http://www.biotamax.com
		Process nutrients more efficiently	
		Degrade organic material	
		Produces plant growth hormones	
		May result in a decreased need for traditional fertilizers	
		Reduced root oxidation	
JumpStart®	*Penicillium bilaiae*	Increased root development	http://www.novozymes.com/en/solutions/agriculture/bioag-in-australia
		Improved nitrogen fixation in legume crops	
		Improved stress tolerance	
		Improved seed quality	
		Earlier, more even maturity	
		Savings on costs, handling, transportation, storage and time requirements compared to more phosphate fertilizer	
		Lower environmental impact	
		Higher yield	
Custom B5™	*Bacillus subtilis, B. laterosporus, B. licheniformis, B. megaterium, B. pumilus*	Enhance soil productivity	http://www.biotamax.com
Ovalis Rhizofertil	*Pseudomonas putida* I-4163	Improve soil quality by mineral amendment and stimulate plant growth	https://www.agriculture-xprt.com/products/ovalis-rhizofertil-biofertilizers-518517

(continued)

Table 2.2 (continued)

Commercial bioformulation	Microbial ingredient(s)	Benefits	Reference
Biofox	*Fusarium oxysporum*	Effective against *Fusarium moniliforme*	www.biofox.com
AgBio	*Streptomyces griseoviridis* strain K61	Prevent *Fusarium* spp., *Alternaria brassicicola*, *Phomopsis* spp., *Botrytis* spp., *Pythium* spp. and *Phytophthora* spp. thatcause seed, root, stem rot and wilt disease of ornamental and vegetable crops	http://www.agbio-inc.com
EcoGuard	*Bacillus licheniformis* SB3086	Effective for prevention of fungal diseases like dollar spot and anthracnose	https://www.harrells.com/uploads/products/labels/ecogua.pdf
PONCHO/ VOTiVO™ mix	*Bacillus firmus* mixed with clothianidin	Provide plant protection against insects and nematode	http://fs1.agrian.com/pdfs/Poncho_VOTiVO_Labelnewa.pdf
Custom N_2	*Paenibacillus polymyxa*	Improve plant's nitrogen nutrition	http://www.biotamax.com
Bioshield™	*Serratia entomophila*	Effective against soil-dwelling grass grub larvae	Jackson (2017)

application methods need to be developed. Although biofertilizers are employed in agriculture practices, they couldn't make huge impact like chemical fertilizers due to lack of educated farmers and repugnance of biofertilizers due to their incompatibility with new soils. Government of individual countries over the globe should encourage organic farming by offering special incentives. Above all successful biofertilizer usage will come into existence where limitations are reduced to an extent that it can compete with the market of chemical industries.

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