Microbial Applications for Sustainable Agriculture

Aftab Afzal and Saeed A. Asad

Abstract Agriculture in the current era is highly dependent on chemical fertilizers, pesticides and weedicides. Excessive applications of these chemicals on crop plants has increased the production cost, jeopardized the environment and has depleted the non-renewable resources. Potential threats to non-renewable resources and soil, water, air environments have led to seek alternative approaches for sustainable crop production and clean environment. To lessen these adversaries, not only scientific community, but industry and farmers are also continuously involved in research, development and adoption of new sustainable technologies. The tiny organisms in rhizosphere have shown their potential to play ubiquitous role in sustainable agricultural development and have been in continuous use since over the last century. In this chapter, different aspects of microbial applications for sustainable agriculture are elaborated. Applications of bacteria-containing biofertilizers, their types and benefits to crops have been discussed. Reports on plant growth promotion through phytohormones, siderophores and enzymes production by rhizobacteria are also detailed. Moreover, sustainable control of plant diseases through biocontrol and amelioration of abiotic stresses including; drought, salinity, climate change and heavy metals by using rhizobacteria are also encompassed in this chapter.

Keywords Applied microbiology · Biofertilizer · Biocontrol · Phytohormone · Siderophore · Abiotic stresses · Drought · Salinity · Climate change

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1 Introduction

Agriculture is the mainstay of economies around the world. The livelihood of people does substantially rely on agricultural products in such economies. Because of intensive nature of today's agricultural practices, it happened to be a high input agriculture and costly as well. This high input agriculture has threatened the whole biogeochemical cycle. The imbalanced use of chemical fertilizers, pesticides, weedicides, fungicides has led to the development of an alarming situation by polluting soil, edibles and atmosphere. The future of agriculture, especially in developing countries is under threat because of a speedy decline in natural resources particularly the reserves of rock phosphate and fossil fuel (Clair and Lynch 2010). As a result, agriculture at time is not sustainable and is leading towards unwise and unjustified use of non-renewable resources. To cope with this alarming situation a sustainable agricultural approach is a need of the hour.

Soil bacteria known as Plant Growth Promoting Rhizobacteria (PGPR) have shown potential for sustainable agriculture. Plant growth-promoting rhizobacteria (PGPR) were first defined by Kloepper and Schroth (1978) as the bacteria inhabiting the rhizosphere, colonizing the roots when they are inoculated on the seeds and have the ability to improve plant growth (Aziz et al. 2012). Recently these eco-friendly microbes have also been recognized as a tool for combating abiotic stresses in crops (Jha and Subramanian 2018). Weller and Thomashow, (1994) reported that rhizosphere is rich source of nutrients and root exudates as a result number and diversity of bacteria is also rich in this zone generally 10–100 times as compare to bulk soil. Bacteria, fungi, actinomycetes, protozoa, and algae generally colonize in surrounding of the roots. However, bacteria are the most predominant microbes existing in the rhizosphere (Kaymak 2010). On the basis of occupancy, PGPR could be categorized in to (i) ectorhizospheric (ii) rhizoplanic or (iii) endo-rhizospheric (Gray and Smith 2005). Later on, PGPR were classified into extracellular plant growth promoting rhizobacteria (ePGPR) and intracellular plant growth promoting rhizobacteria (iPGPR) (Viveros et al. 2010). The ePGPRs may exist in the rhizosphere, on the rhizoplane or in the spaces between the cells of root cortex while iPGPRs locate generally inside the specialized nodular structures of root cells. Out of total rhizospheric bacteria, a small fraction (2–5%) may be plant growth promoters (Antoun and Prevost 2005). The PGPRs have diversified bacterial species, however the predominant are species of *Bacillus* and *Pseudomonas* (Podile and Kishore 2006). These microbial populations, when inoculated, enhance plant growth which is a proven fact (Nehra 2011; Bhattacharyya and Jha 2012).

The success of inoculation depends on (i) survival of inoculated bacteria on seed, (ii) ability to reproduce in the spermosphere (region around seed), (iii) ability to attach to the phyllo sphere and (iv) the ability of inoculated bacteria to colonize the extending root system (Kloepper 1993) and of course the inoculation method. Most of the time, PGPR fail in the field due to incapability to survive and colonize plant roots (Bloemberg and Lugtenberg 2001). Basically this colonization process is controlled by a variety of bacterial traits and specific genes. These traits include; motility, chemotaxis in response to seed and root secretions, production of pili or fimbriae, production of cell surface components, protein secretions and quorum sensing. Now the mutants are being generated to study the expression of these traits in order to comprehend the involvement of these traits in colonization process (Lugtenberg et al. 2001). To detect gene expression during colonization, reporter transposons and in vitro expression technology (IVET) are being employed (Roberts et al. 1998; Rainey 1999). The location of individual rhizobacteria and its metabolic activity in the rhizosphere can be monitored by using molecular markers such as green fluorescent protein, gfp, rfp, lux, gus or fluorescent antibodies and by using confocal laser scanning microscopy (Bloemberg et al. 2000). By combining these techniques with an rRNA-targeting probe it was revealed that bacteria colonized at the root tip were most active (Lübeck et al. 2000).

The PGPR can increase the plant growth either directly or indirectly (Glick 1995; Akhtar and Siddiqui 2009) through various mechanisms. The direct modes of action include; nitrogen fixation, solubilization of phosphorous and various other minerals (e.g. K, Zn), phytohormone production and reducing the level of ethylene by producing ACC- deaminase (Vessey 2003; Ahemad and Kibret 2014). The rhizobacteria with these direct mechanisms act as biofertilizers or Phytostimulators in the absence of plant pathogens (Lugtenberg and Kamilova 2009). On the other hand, some PGPR improve plant growth indirectly by suppressing plant pathogens (especially soilborne plant pathogens) using different mechanisms (Labuschagne et al. 2010). So, the beneficial rhizobacteria can promote plant growth as well as plant health through environment friendly way (Calvo et al. 2014). For decades, a large number of PGPRs have been investigated and some of them have been marketed as biofertilizers/bio pesticides, including the Genera: *Pseudomonas*, *Bacillus*, *Azosprillum*, *Azobacter*, *Enterobacter*, *Klebsiella*, *Variovorax* and *Serratia* (Glick 2012).

The interactions of PGPR with plants have been used commercially (Podile and Kishore 2006) and is very applicable for sustainable agriculture. These bacteria have been reported to interact with a variety of crop plants including maize, wheat, oat, barley, peas, canola, soy, potatoes, tomatoes, lentils, radicchio and cucumber (Gray and Smith 2005). There is a strong growing market for microbial inoculants worldwide with an annual growth rate of approximately 10% (Berg 2009). So it's a scientifically and technologically proven fact that PGPR can be applied for sustainable crop production and for environment friendly agricultural practices. To highlight the applied aspects of microbes and their potential as biological agents for fertilization and disease control a thorough review has been done. In current review, five different applications of microbes (bacteria) for sustainable agriculture have been discussed. These applications included: (i) biofertilizers, when they are used to enhance nutrient availability (ii) Phytostimulators, helping in plant growth via plant growth regulators (iii) bio pesticides, while protecting plants from phytopathogens (iv) as Bioremediators, their application for cleaning the soil polluted with heavy metals and (v) abiotic stress ameliorators, when rhizobacteria are being employed for reducing the risk of abiotic stress conditions.

2 Historical Perspectives

The involvement of rhizobacteria in plant growth promotion is historical and inoculation of plants with useful bacteria is not a new idea, it goes back to many centuries. The benefits of growing legumes before non-legumes were well known to farmers by experience. In late nineteenth century, the rhizobium inoculants were used in USA for the first time as a biological fertilizer named as ‘Nitragin’ and subsequently this practice was used with legumes in many countries (Bagnasco et al. 1998). Kloepper and Schroth (1978) for the first time used the term “plant growth promoting rhizobacteria (PGPR)” for these beneficial bacteria.

The practice of mixing “naturally inoculated” soil with seeds became a recommended method of legume inoculation in the USA by the end of the nineteenth century (Smith 1992). A decade later, the *Rhizobium* sp. was registered for plant inoculation, as the first patent (“Nitragin”) (Nobbe and Hiltner 1896). Ultimately, rhizobia inoculation to legumes became common practice. Many small companies are producing *Rhizobium* inoculants in different countries since centuries. In Brazil for example nitrogen fertilization is done through Rhizobia (Döbereiner et al. 1994). Similarly, rhizobial inoculants were contributing significantly to legume production in Australia, New Zealand, Egypt, South Africa, North America, Eastern Europe and somewhat in Southeast Asia. In the USA, Brazil, and Argentina however inoculation of soybean made a major agricultural impact. Inoculant technology has not been much successful in Asia, Africa, and Central and South America due to poor quality of inoculants (Eaglesham 1989). In the 1930s and 1940s *Azotobacter* inoculation was done on a large scale in Russia. But this practice could not bring noticeable results, so it was abandoned at that time (Rubenchik 1963). In 1930s *Bacillus megaterium* was used for phosphate solubilization on large scale in Eastern Europe (Macdonald 1989). Two major advancements in biofertilizer technology occurred in the late 1970s (1) Plant growth and yield of non-legumes was improved significantly with inoculation of *Azospirillum* (Döbereiner and Day 1976), due to its direct effect on plant metabolism (Bashan and Holguin 1997), and (2) *Pseudomonas fluorescens* and *P. putida* were largely investigated and proven to be effective biocontrol agents (Défago et al. 1992; Kloepper and Schroth 1981; Glick 1995; Glick and Bashan 1997). At the end of twentieth century other bacteria like *Bacillus*, *Flavobacterium*, *Acetobacter*, and several other microorganisms were also investigated to be potential PGPR (Kloepper 1994; Tang 1994; Tang and Yang 1997). The first commercial inoculant of PGPR (Free living or associative rhizobacteria) was only possible at the end of last century (Fages 1992; Tang 1994; Tang and Yang 1997).

3 Application of Microbes as Nutrient Mobilizers (Biofertilizers)

Biofertilizer is a substance which contains living microorganisms and promotes growth by increasing the supply or availability of primary nutrients to the host plant, when applied to seeds, plant surfaces, or soil (Vessey 2003). Bio-fertilizers provide "eco-friendly"organic agro-input. Biofertilizer technology has shown promise for integrated nutrient management through biological N fixation (BNF) and improving P availability to crops. Bio-fertilizers, containing *Rhizobium*, *Azotobacter*, *Azospirillum* and blue green algae (BGA) have been in use since a long time. Rhizobium inoculant is used for leguminous crops. One of the rhizobacteria '*Azotobacter*' is used for the inoculation of crops like wheat, maize, mustard, cotton, potato and other vegetable crops. Another very promising rhizobacteria *Azospirillum* is generally recommended for inoculation onto sorghum, millets, maize, sugarcane and wheat. Nitrogen fixing cyanobacterial genus, *Nostoc* or *Anabaena* or *Tolypothrix* or *Aulosira* (Blue green algae) are used as inoculations for paddy crop. One of the blue green algae '*Anabaena'* can fix N up to 60 kg/ha/season in association with water fern Azolla. Biofertilizers can be classified on the basis of basic nutrient they provide to the crops. Three major classes are described in the paragraphs below.

3.1 Nitrogen Biofertilizers

Nitrogen (N) is the most essential and primary macronutrient for plants. Nitrogen-fixing microorganisms can transform atmospheric nitrogen into available nitrogen (inorganic compounds usable by plants) through conversion of N_2 into NH_3. These microorganisms play a pivotal role in N cycle, because more than 90% of N fixation is carried out by these organisms (Encyclopedia Britannica 2018). Generally, there are two kinds of N fixing microorganisms (Bacteria). The first kind, symbiotic (mutualistic) bacteria, includes *Rhizobium* (symbiotic with leguminous plants) and *Frankia* (symbiotic with actinorhizal plants). The second type, non-symbiotic bacteria may be free-living (e.g., *Azotobacter*, *Beijerinckia*, *Clostridium,* cyanobacteria (*Anabaena* and *Nostoc*) *Gluconacetobacter diazotrophicus* and *Azocarus*) or associative/endophytic (e.g., *Azospirillum*) (Bhattacharyya and Jha 2012).

The first bacterium of this type was isolated by Beijerinck from the nodules of legumes in 1888 and named as *Bacillus radiocicola*. However, Frank (1889) renamed it as *Rhizobium leguminosarum* (Fred et al. 1932), which was retained in *Bergey's Manual of Determinative Bacteriology* (Holt et al. 1994). Salvagiotti et al. (2008) while analyzing the data of publications from 1966 to 2006, derived from 108 field studies in 17 countries mostly related to soybean N fixation and fertilization, concluded that biological N fixation has a major contribution (50–60%) in soybean N fertilization; however, increasing N fertilizer rates badly affect N fixation.

Rhizobium inoculation on other legumes is also beneficial and helps in profound nodulation and increasing yield of important legumes.

3.1.1 Non-symbiotic N-Fixers

3.1.1.1 Free-Living Nitrogen Fixers

Free living bacteria (rhizospheric bacteria) have the capability to inhabit soil and biologically fix N, without any host. *Azotobacter*, *Beijerinckia*, *Clostridium, Cyanobacteria* (*Anabaena* and *Nostoc*) *Gluconacetobacter diazotrophicus* and *Azocarus* are examples of free living N fixers. Vadakattu and Paterson (2006) reported that free-living N fixers contributed 20 kilograms N per hectare per year in an intensive wheat rotation farming system in Australia (30–50% of the total needs). Non-symbiotic N_2 fixation (by free-living bacteria in soils or associated with the rhizosphere) is important in providing some amount of N particularly in low input cropping systems worldwide. Due to use of indirect methods of measurement of N fixed, non-symbiotic N fixers could not get good name, however isotope-based direct methods indicate agronomically significant amounts of N_2 fixation both in annual crop and perennial grass systems. New molecular technologies should be employed to determine the potential of free living N fixers. This knowledge should assist the development of new plant-diazotrophic combinations for specific environments and more sustainable exploitation of N_2-fixing bacteria as inoculants for agriculture (Roper and Gupta 2016).

3.1.1.2 Associative Nitrogen Fixers

Some bacterial species live in close association with host plant, either on the surface of roots or inside the root (in intercellular spaces). Species of *Azospirillum* are peculiar example of such species which form association with important cereal crops such as; rice, wheat, corn, oats, and barley. These bacteria are able to fix atmospheric Nitrogen which is useful for the plants. It is reported that such bacteria can fix upto 52 mg N_2 g^{-1} malate (Stephan 1979). One of the most used plant growth promoting bacteria (PGPB) is *Azospirillum brasilense.* This bacterial specie has been used in Brazil, Argentina, Mexico, India and Europe. Statistically significant increases in yield varying from 5% to 30% have been achieved as a result of inoculation of *A. brasilense*. Analyses of field experiments have shown that 60–70% of inoculation with Azospirillum was successful (Yaacov and Robin 1995). Associative N fixation (ANF) proved to be an important source of N to unfertilized switchgrass and to temperate grasslands. This was concluded by Roley et al. (2018) when he used to measure N fixation potential of associative bacteria.

Fig. 1 Extensive nodulation of a peanut root after inoculation with *Bradyrhizobium* strain 32H1. (Source: Wagner 2011)

3.1.2 Symbiotic Nitrogen Fixers

Symbiotic N_2-fixing bacteria include members of the family rhizobiaceae (*Rhizobium, Sinorhizobium, Bradyrhizobium, Mesorhizobium* and *Azorhizobium*, collectively termed as 'rhizobia' which forms symbiosis with leguminous plants (Zahran 2001). Alfalfa, beans, chickpea, clover, cowpeas, lupines, peanut, soybean and vetches are important legumes used in agricultural systems. About 50% of the global area devoted to legumes is under the cultivation of soybean and represent 68% of the total global legume production (Vance 2001). The symbiotic nitrogen-fixing bacteria (Rhizobia) enter the root hairs of host plants, where they multiply and stimulate formation of root nodules. A typical example of nodule formation in peanut is shown in Fig. 1. The nodules are the sites of N fixation where it is reduced to ammonia in presence of a complex enzyme system, the 'Nitrogenase'. The ammoniac N is available for plant nutrition. This natural process is expedited by application of inocula of rhizobial strains to seeds of legume crops for abundant nodule formation and maximum plant growth (Encyclopedia Britannica 2018; Laranjo et al. 2014).

A water fern *Azolla* also form symbiotic relationship with a cyanobacterium *Anabaena Azolla*. *Azolla* fronds allow the *Anabaena* to colonize at the cavities formed at its base. After colonization the cyanobacteria fix a plenty of N in its specialized cells called heterocyst. This symbiotic relationship is being employed as biofertilizer for at least 1000 years in wetland paddies in Southeast Asia. During the growing season, up to 600 kg N ha^{-1} $year^{-1}$ is fixed by *Azolla* "blooms" in rice paddies (Postgate 1982; Fattah 2005).

Actinomycetes, *Frankia alder* (Alnus sp. actinorhizal plants) is another example of symbiotic association (Benson and Silvester 1993). The tree genera such as the temperate-region *Alnus* and *Myrica*, the arid-region *Acacia*, and the tropical-region

Casuarina and *Ceanothus* are typical examples of actinorhizal plants making symbiotic association with actinomycetes (*Frankia*). In the latter region, efforts are being made to develop a crop-rotation system with agro-forestry that utilizes leguminous trees (e.g., *Leucaena leucocephala*) able to incorporate significant amounts of nitrogen into the soil for the subsequent benefit of crop production. This type of association needs to be investigated and exploited further for its potential use in sustainable agriculture system.

3.2 Phosphate Solubilizing Biofertilizers

Phosphorus (P) is the second most essential macronutrient for plants after nitrogen (N), and is applied to soil in the form of phosphate fertilizers. However, most of the P applied to soil or native soil P becomes unavailable to plants because it forms chemical bonding with the metal ions present in the soil (Ca^{++}, Fe^{++} or Al^{+}), thus forming insoluble compounds (Malboobi et al. 2009). Phosphate solubilizing bacteria (PSB) are beneficial bacteria capable of solubilizing inorganic phosphorus from insoluble compounds (Chen et al. 2006). This is one of the most important traits of the rhizospheric bacteria and plays a significant role in P nutrition of crop plants. It is generally accepted that these bacteria solubilize P by producing low molecular weight organic acids which can chelate the cations chemically bonded to P thus releasing P from these insoluble inorganic compounds. Such bacteria (PSB) are being used for preparing biofertilizers for increasing P availability to plants. The major issue is to optimize the P fertilizer rates without compromising the yield and to minimize P loss from soil. These bacteria have attracted the attention of agriculturists for sustainable crop production (Zandi and Chalaras 2014). About 50% of the crop requirement of phosphatic fertilizer can be saved by using PSB with rock phosphate (Saleem et al. 2013). Accordingly, it is reported that P fertilizer application can be reduced to 50% by co-inoculating the phosphate-solubilizing bacteria (PSB) with PGPR without compromising crop yields (Jilani et al. 2007; Yazdani et al. 2009). Inoculation of seeds with PSB can reduce the use of P fertilizers upto 50% (equivalent to 30 kg P_2O_5 ha^{-1}). Alternatively, fertigation or hydroponic methods can also be employed to inoculate PSB to fields. *Bacillus megaterium, Pseudomonas putida* (P13), *Pantoea agglomerans* (P5), *Microbacterium laevaniformans* (P7) strains are highly effective for insoluble phosphate solubilization. A consortium of bacteria is more effective and solubilizes phosphate at faster rate than single strain inoculum. Peter et al. (2016) used a consortium of four PGPR (marketed as Mammoth P) and reported that it solubilizes phosphate at much faster rate as compared to any strain inoculated alone. Romano et al. (2017) reported recently that bacteria inhabited under phosphorus deficient conditions produce iron-chelating molecules (Siderophores). It was suggested by the author that some bacteria can interact with both of these elements (Phosphorus and iron) and can improve the availability of these essential and limiting plant nutrients.

4 Biofertilizers Impacts on Crop Yield and Nutrient Uptake

According to a meta-analysis conducted recently (Schutz et al. 2018), Arbuscular Mycorrhizal Fungi (AMF), and other biofertilizers with N fixing and P solubilizing capability are most effective in increasing crop yield and nutrient uptake. Co-inoculation of bacteria with both traits (N fixation and P solubilization) is more beneficial for improving crop yield as compare to single inoculation (Fig. 2). Similarly, across all crop categories (Table 1), an average yield increase of 16.2 ± 1.0% was recorded by inoculation with biofertilizers as compared to non-inoculated controls (Fig. 3a). It was also noted that legumes showed greater response upon inoculation and response of root crops was relatively poor. Phosphorus use efficiency (PUE) and nitrogen use efficiency (NUE) was also improved as a result of biofertilization (7.5 ± 0.8 kg yield per kg P and 5.8 ± 0.6 kg yield per kg N fertilizer). The nutrient use efficiency was most profound in legumes as compared to other crops (Fig. 3b, c).

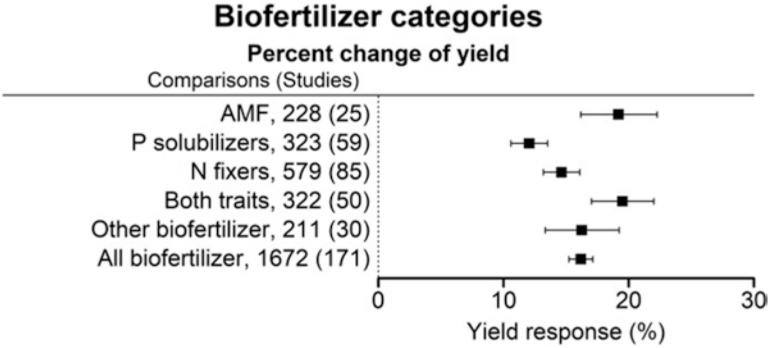

Fig. 2 Percentage change of yields in response to the application of various categories of biofertilizers. Mean values and 95% confidence intervals of the back-transformed response ratios are shown. AMF and N-fixers in combination with P solubilizers showing more pronounced effect. (Adapted from Schutz et al. 2018)

Table 1 Crops included in meta-analysis

Category	Crops included
Cereals	Barley, durum wheat, rice, spring wheat, winter wheat, pearl millet, maize, sorghum, kamut, silage maize, ryegrass, finger millet
Legumes	Blackgram, chickpea, peanut, horsegram, kidney bean, mung bean, fenugreek, lentil, snap bean, soybean, runner bean, pigeon pea
Root crops	Garlic, potato, turmeric, sugar beet, cassava
Vegetables	Eggplant, tomato, cabbage, watermelon, pepper, okra, cucumber, melon
Other crops	Dill, anise, rapeseed, cotton, sesame, fennel, coriander, sunflower, mustard, sugarcane

Source: Schutz et al. (2018)

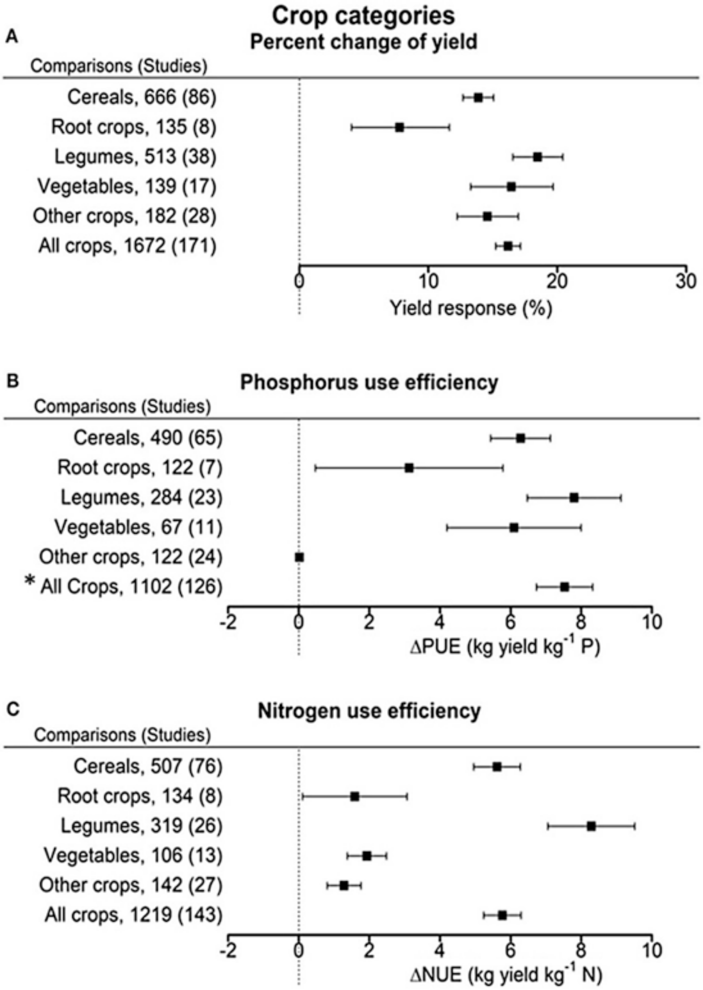

Fig. 3 Percentage change of yields (**a**), change in phosphorus use efficiency (PUE) (**b**), nitrogen use efficiency (NUE) (**c**), in response to biofertilizer application. ∗The high value for all crops is caused by the outlier calculation that resulted in different pairs being excluded for the full sample and the sub-samples. (Adapted from Schutz et al. 2018)

5 Microbial Applications as Plant Growth Promoters (Phytostimulators)

Soil microorganisms are ubiquitous to impart myriads of benefits for plant growth and health leading to successful survival of flora. These tiny creatures exhibit unique characteristics which directly or indirectly regulate some core functions of plants (Berg 2009). Diazotrophs including; *Rhizobium* and *Azospirillum* significantly improve plant growth while producing phytohormones, nitrogen fixation, phosphate solubilization. While several bacterial (e.g. *Pseudomonas*) and fungal (*Trichoderma* and *Coniothyrium*) genera are well studied for their involvement in improving plant health and barring different plant diseases. Plant beneficial microorganisms including plant growth promoting rhizobacteria, mycorrhizal fungi and antagonists are the special creatures for partial substitution or possible replacement of artificial chemicals. These microbes or microbial products can be successfully employed to meet the increasing food demand without any toxicity or environmental concerns (Glick 2012).

Mycorrhizal fungi living in symbiotic association with plants are of two types; ectomycorrhizae and arbuscular mycorrhizae (AM) where the later are most abundant in soil environments. The AM form symbiotic relationship with plants (Willis et al. 2013). These fungi play pivotal role in enhancing the productivity of several field crops by penetrating deeply in to the soil, for more nutrients and water especially under nutrient and water limiting environments (Guo et al. 2010) than non-mycorrhizal plants. Mycorrhizae promote plant growth via secretion of metabolites including; amino acids, phytohormone, vitamins and/or through speeding up the mineralization processes. They also enhance the supply of phosphate, where around 80% of phosphorous taken up by mycorrhizal plant is supplied by AM fungi (Marschner and Dell 1994). Moreover, these fungi also help plant to take up other macro and micro nutrients including N, Zn, K, Cu and Mg especially when these nutrients are in less soluble forms.

Microorganisms influence plant growth through; secretion of metabolites, enzymes, inducing systemic resistance, protecting from pathogens and diseases and most importantly from environmental stresses (Shameer and Prasad 2018). Regardless of their modes of actions, these microorganisms could involve anyone or multiple of the following metabolites for enhancing plant growth and deterring pathogenicity. Paragraphs below detail the involvement and mechanisms through which these microorganisms alleviate the plants against stresses.

5.1 Phytohormone Producers

Among many of the physiological attributes, phytohormone production/metabolization ability of these tiny creatures is well recognized (Okon and Labandera-González 1994). Benefits imparted by microorganisms are actually an outcome of multiple physiological activities occurring at the same time. This series of activities idea originates from the “additive hypothesis” proposed in the last decade of previous century (Bashan and Levanony 1990; Bashan and de Bashan 2010). Phytohormone production by microorganisms is one of the mechanisms to explain this hypothesis. Almost all of the microbial genera involved in plant growth are capable to produce or metabolize phytohormones. All bio inoculants or biofertilizers including; *Bacillus*, *Azospirillum, Pseudomonas, Enterobacter, Erwinia, Azotobacter, Serratia, Klebsiella, Alcaligenes, Flavobacterium, Arthrobacter, Burkholderia, Bacillus,* *Acinetobacter, Azotobacterium, Xanthomonas* and *Rhizobium* (Bhattacharyya and Jha 2012) have demonstrated phytohormone production under controlled and natural settings.

Phytohormones produced by different microbial genera and physiological functions attributed to them are detailed in Table 2. Auxins, gibberellins, cytokinins, ethylene and abscisic acid are the most studied microbial hormones involved in the plant growth and development one way or the other. *Auxins* or naturally occurring auxin molecule, indole-3-acetic acid (IAA) are known to induce cell elongation in the subapical regions of the stem. The major attributes of these hormones vary from lateral and adventitious roots initiation, root/shoot elongation, photo and gravitropism and cell division (Teale et al. 2006). Infact, *Azospirillum* has proved to be a model species for elaborating and understanding the role of auxins in plant growth and even in maintaining plant and rhizobial interactions (Berg 2009). Despite a wide range of physiological activities attributed to auxins produced by *Azospirillum*, only few commercial bio inoculants have been formulated containing *Azospirillum* sp. (Cassán et al. 2014) Majority of the plant growth promoters and bio fungicides respectively contain *Bacillus* and *Trichoderma* as is evident from data in Table 3. As described in previous paragraphs, direct promotion of plant growth by microbial inoculants is through secretion of phytohormones. *Acetobacter diazotrophicus*, *Azospirillum* sp. *Azospirillum lipoferum* and *Azospirillum brasilense* all have been well studied for producing indole3-acetic acid (IAA), ethylene, gibberellic acid (GA3) and abscisic acid (ABA) respectively (Bastian et al. 1998; Strzelczyk et al. 1994). Auxin production by *Azospirillum* in the root zone is considered as the major factor for enhancing plant growth and development of root system in Gramineae plants. Moreover, these auxins also regulate other rhizosphere bacteria such as nodule formation and improve the symbiotic relationships between rhizobia and legumes. Therefore, any alteration in the concentration of auxin could severely impact nodule formation (Mathesius et al. 1997). A study conducted by Burdman et al. (1996) revealed that *Phaseolus vulgaris* seedlings inoculated with *A. brasilense* exhibited increased root flavonoids and enhanced expression of nod gene in *Rhizobium* compared with control. Auxins facilitate adventitious roots penetration thereby providing more nutrients for bacterial and plant growth. These characteristics make auxins key metabolite to regulate plant-microbe interactions in terms of Phyto stabilization and pathogenicity (Ahemad and Khan 2012a).

Another important phytohormone, Gibberellic acid (GA) alleviate the drought stress and play crucial role in the initiation of flowering and hypocotyls elongation (Yamaguchi 2008; Vandenbussche et al. 2005). Major physiological development in plants from seed germination to photosynthetic activity, light interception, nutrient use efficiency, fruit growth and delayed dormancy in major plant genera are attributed to the presence of gibberellic acid. This hormone actively relives the plant against abiotic stresses and maintains the continued growth and development of stressed plant organs (Iqbal et al. 2011). GAs produced by *Bacillus* and *Azospirillum* inoculants resulted in increased uptake of N in wheat plants thereby alleviating the plants against drought and salinity stresses (Shaddad et al. 2013). Other plant bacteria, *Pseudomonas*, *Bacillus* and *Azotobacter* and *actinomycetes* were reported to

Table 2 Phytohormones and other plant beneficial metabolites produced by different microorganisms and their effects on plant growth/health. Data presented below is research data collected from in vitro experimentation

Microorganisms/ biofertilizers	Phytohormones/ metabolites produced by beneficial microbes	Influence on plant growth/ health	References
Bradyrhizobium japonicum	Auxins (IAA), siderophores, antibiotics, cell wall degrading enzymes	Phosphate solubilization, improved germination and increased biomass of plant	Chandra and Pareek (2007) and Afzal and Bano (2008)
Mycobacterium	Auxins (IAA)	Increased plant resistance against pathogens	Egamberdiyeva (2007)
Pseudomonas	Siderophores	Inhibited fungal growth on plant roots	Nowak et al. (1994)
Fluorescens			
Bacillus sp.	Auxin (IAA) and spore formation	Increased shoot length by up to 40% and increased the number and length of adventitious roots	Ahmed and Hasnain (2010)
Burkholderia	Auxin (IAA), reduced acetylene to ethylene	Improved germinations percentage and increased rice yield up to 23%	Govindarajan et al. (2008)
Bradyrhizobium sp.	HCN, Auxins (IAA) and siderophores.	Phosphate solubilization, significantly increased plant biomass and wheat yield	Afzal and Bano (2008)
Sphingomonas	Gibberellins (GAs)	Enhanced the plants competitive ability for space and nutrients	Innerebner et al. (2011) and Khan et al. (2014)
Enterobacter cloacae	Auxins (IAA)	Phosphate solubilization	Bhattacharyya and Jha (2012)
Serratia mercescens	Auxin, HCN and siderophore production	Significantly improved plant biomass	Selvakumar et al. (2008)
Acinetobacter sp.	Auxins, ACC deaminase and producing antifungal metabolites	Phosphate solubilization	Indiragandhi et al. (2008)
Actinomycetes	Cell wall degrading enzymes (e.g. cellulases)	Induced resistance against soil born pathogen, *R. solani*	Schmidt et al. (2001)
Enterobacter asburiae	Auxins (IAA), HCN, exopolysaccharides, and siderophores	Phosphate solubilization	Ahemad and Khan (2012b)
Streptomyces	Auxins (IAA) and siderophores	Resistance against soil borne pathogens	Verma et al. (2011)
Rhizobium leguminosarum	Cytokinins, antibiotics and cell wall degrading enzymes	Enhanced minerals and P solubilization for plant uptake	Zahir et al. (2010)
Azotobacter chroococcum	Gibberellins, kinetin, IAA	Phosphate solubilization	Ahemad and Kibret (2014)

Table 3 List of commercially available biocontrol products

Microorganism's type	Biocontrol Agent	Commercial mame/ company	Target pathogen
Bacteria	*Agrobacterium radiobacter*	Galltrol/AgBioChem Inc. USA	Crown gall disease caused by *Agrobacterium tumefaciens*
		www.agbiochem.com	
		Nogall/Bio Care Technology, Australia	Crown gall disease caused by *Agrobacterium tumefaciens*
		http://bio-caretechnology.com/	
	Bacillus sp.	Companion/Growth Products Ltd. NY, USA/	*Rhizoctonia*, *Pythium*, *Fusarium*, and *Phytophthora*
		http://www.growthproducts.com	
		HiStick N/T/Helena Agri-Enterprises, USA	*Fusarium, Rhizoctonia, Aspergillus*
		https://helenaagri.com	*Rhizoctonia solani, Fusarium spp.,*
		Kodiak/ Bayer crop Science, USA	*Alternaria spp., and Aspergillus spp.* that attack roots powdery mildew, downy mildew,
		https://www.bayer.com	
		Serenade/Bayer crop Science, USA	Cercospora leaf spot, early blight, late blight, brown rot, fire blight
		https://www.cropscience.bayer.us	
		YieldShield/Bayer crop Science, USA	Soil borne fungal pathogens causing root diseases
		https://www.cropscience.bayer.us	
		Rhizo-Plus/Disha Chemicals, India	*R. solani*, *Fusarium spp. Alternaria spp.*, *Sclerotinia* and *Verticillium*
		http://www.theagrihub.com	
	Pseudomonas sp.	BioJet Spot-Less/Eco Soils Systems, Inc., San Diego, Ca	Dollar spot, Anthracnose, *Pythium aphanidermatum, Michrochium patch* (pink snow mold)
		https://www.nasdaq.com	
		Bio-save/Jet Harvest Solutions, Florida, USA	*Botrytis cinerea*, *Penicillium spp.*, *Mucor pyroformis, Geotrichum candidum*
		https://jetharvest.com	
		BlightBan/Nufarm Americas Inc. USA	*Erwinia amylovora*, and russet inducing bacteria
		http://www.nufarm.com	
		Cedomon/Nutrilita, Lithuania	Leaf stripe, net blotch, *Fusarium* sp., spot blotch, leaf spot
		http://www.nutrilita.lt	

(continued)

Table 3 (continued)

Microorganism's type	Biocontrol Agent	Commercial mame/ company	Target pathogen
		Conquer/Mauri Foods, Australia	*Pseudomonas tolassii*
		http://www.maurianz.com	
		Victus/Sylvan Spawn Laboratories, USA	*Pseudomonas tolassii*
		https://www.manta.com	
Fungi	*Ampelomyces quisqualis*	AQ10/Bioguard, CBC Group, Europe	Powdery mildew
		http://www.biogard.it	
	Candida oleophila	Aspire/Ecogen Inc. USA	*Botrytis* spp., *Penicillium* spp.
		https://www.bloomberg.com	
	Coniothyrium minitans	Contans WG/Intercept WG/Bayer Crop Science, South Africa	*Sclerotina sclerotiorum* and *S. minor*
		https://www.cropscience.bayer.co.za	
	Myrothecium verrucaria (killed)	DiTera/Valent, North America	Parasitic nematodes
		https://www.valent.com	
	Trichoderma sp./*Gliocladium* sp.	Plantshield/Rootshield/T-22 Planter box Soilgard Primastop/Bioworks, NY, USA	Pythium spp., Rhizoctonia solani, Fusarium spp.
		https://www.bioworksinc.com	

Adopted and modified from Gardener and Fravel (2002)
These biocontrol products are registered with the environment protection agency (EPA) of USA

produce GAs which significantly influenced nutrient uptake and growth improvement of inoculated plants of wheat as compared to control (Shaddad et al. 2013).

Cytokinins play key role in cell division, primary root growth and senescence. In fact, many of the cytokinins genes are expressed in roots highlighting their involvement in root development. Wide range of microbial species produce cytokinins in plant roots enhancing their growth and development thereby resulting in more nutrients uptake in plants. Cytokinins produced by *Bacillus megaterium* had a significant role in promoting plant growth as noted by Ortíz-Castro et al. (2008). These bacterial cytokinins influenced the root architecture, increased root hair length and lateral root formation. Endophytic bacteria, *Bacillus* isolated from *Arabidopsis thaliana* exhibited the potential to increase the root/shoot growth as compared to control plants (Wang et al. 2015).

The plant hormone, ethylene is recognized as the regulator of plant growth and development. In response to environmental stresses, plants up regulate the production of ethylene to initiate the defense mechanisms, but increased production of ethylene will induce a range of abnormalities including growth inhibition and delayed flowering. This increased level of ethylene can be easily reduced by using chemicals such as; cobalt ion (Co^{2+}) and silver ion (Ag^{+}), but because of their toxicity and higher price make them last choice for farmers. Hence keeping the balance in ethylene production is of paramount importance for agricultural crops productivity and microbes can potentially modulate the ethylene production. For example, microorganisms decrease the level of ethylene through ACC-deaminase enzyme production which is widely reported in fungi, bacteria and stramenopiles (Nascimento et al. 2014). Worth noting that ethylene reduction by microorganisms is not always in the favor of plant. For example, under saline environment, ethylene reduces root growth to avoid salt pollution. Under such environment, ethylene reduction by microbes may increase root growth but may also result in disastrous effects on overall growth of plant and food chain toxicity (Desbrosses et al. 2009).

Like ethylene, abscisic acid is also called stress hormone, synthesized in plants in response to environmental stresses and expressing the stress resistance genes (Sah et al. 2016). ABA ameliorates the salinity stress by regulating the photosynthetic apparatus and is also important hormone for mediating the plant-microbial interactions as many plant growth promoting bacteria such as; *P. fluorescens, A. brasilense, Variovorax paradoxus* and *B. licheniformis* produce ABA (Dodd et al. 2010; Cohen et al. 2015). A study by Cohen et al. (2015) revealed that plant inoculated with abscisic acid producing PGPR, *P. fluorescens* enhanced the ABA hormone thereby increasing their ability to withstand better under drought conditions as compared to uninoculated controls. Moreover, inoculation with PGPR decrease the hormone accumulation in roots thereby regulating shoot/root and root/shoot hormonal signaling and resulting changes in ABA may reduce the plant sensitivity to water deficiency. Qin et al. (2016) reported that tomato plants inoculated with halotolerant PGPR exhibited enhanced growth. Role of PGPR to influence ABA concentrations makes it an ideal choice for inducing resistance against abiotic stresses in plants and withstand harsh environments without jeopardizing the yield potential.

5.2 Siderophore Producers

Siderophores are low molecular weight iron chelating metabolites having great affinity for iron. Out of approximately 500 known siderophores, chemical formulae of >200 have been worked yet (Shameer and Prasad 2018). These water soluble compounds can be grouped in to extracellular and intracellular ones (Hider and Kong 2010). In fact, siderophores are the key instrument to release unavailable iron and make it available to the living biota (Rajkumar et al. 2010). Iron mostly exists in Fe^{3+} form which remains insoluble and hence unavailable for plant uptake. Siderophores released by microorganisms' act as iron solubilizing agents especially under iron-limiting conditions (Ahemad and Khan 2012a).

Microbes used in the formulations of biofertilizers are both gram positive and gram negative and interestingly both forms of bacteria are equipped with the ability to reduce Fe^{3+} to Fe^{2+} in their membranes. This reduced form of iron is released by siderophores in to the cell making it available to plants via gating channels connecting outer and inner membranes of the cell (Mahanty et al. 2017). Various mechanisms through which plants take up iron liberated by bacterial siderophores include either direct uptake of Fe-siderophore complexes, or through chelating/releasing iron and ligand exchange reaction (Thomine and Lanquar 2011). Model plant, *Arabidopsis thaliana* accumulated an increased level of Fe synthesized by *Pseudomonas fluorescens* from Fe-pyoverdin complex which significantly improved plant growth compared with control plants (Parray et al. 2016). *Pseudomonas* produce a mixture of Fe-pyoverdin which has key role for iron uptake by *A. thaliana.* Fe availability is of paramount importance especially for plants under stressed environments, where these siderophores alleviate the plants against heavy metal stresses (Rajkumar et al. 2010). Several studies investigating the benefits of siderophores revealed that plants were able to take up the iron once inoculated with siderophore producing *Pseudomonas* bacteria (Hider and Kong 2010). Mung bean (*Phaseolus vulgaris*) plants inoculated with these bacteria in iron deficient soils, showed less chlorotic symptoms than control plants. Iron supply is imperative for plants exposed to heavy metal stress, where siderophores produced by microorganisms alleviate heavy metal stresses to plants. This siderophore triggered uptake of iron help plants to survive under Fe-limiting conditions (Guerinot and Ying 1994).

5.3 Enzymes Production

Plant diseases/pathogens have deleterious effects on agricultural productivity and pose a multiplying challenge for ensuring the food security. Amongst those pathogens, soil borne pathogens are the most devastating agents hampering the agricultural productivity (Newbery et al. 2016; Kashyap et al. 2017). According to Savary et al. (2012), direct yield losses because of diseases and weeds are approximately 40% of agricultural produce. For controlling these plant diseases, use of pesticides has rewarded in terms of yield increase but compromising on the quality as well as heralding challenges for sustainable production. To substitute or lessen the use of chemicals, plant beneficial microorganisms have imparted marvelous benefits in terms of biological control of pathogens. This is perhaps due to the fact that onset of green revolution and indiscriminate uses of herbicides, pesticides and chemical fertilizers has posed several adverse effects to the environment (Tilman 1998). Many of these chemicals have been reported to be carcinogenic (Damalas and Eleftherohorinos 2011). To lessen the adversaries triggered by these toxic means of controlling pathogens and diseases, biological control is employed for controlling agricultural pests mainly for economic and sustainability. Various microorganisms exhibit hyperparasitic action to hydrolyze pathogen cell wall through extracellular enzymes (Chemin and Chet 2002). For instance, chitinase produced by *Serratia plymuthica* significantly reduce spore germination of *Botrytis cinerea* (Gaffney et al. 1994). Soil bacteria perform excellently to control soil borne plant pathogens. *Bacillus* controls various fungal diseases through secretion of various lytic enzymes which inhibit mycelial growth of various fungal species (Yu et al. 2002). Overall three mechanisms including: the secretion of antibiotics, competing for nutrients and space and mycoparasitism by microorganisms suppress the pathogen growth. Interestingly, many of the *Bacillus* strains exhibit mycoparasitic characteristic because of their tendency towards physical interactions (Abdullah et al. 2008). Many plant growth promoting rhizobacteria such as, *Pseudomonas, Staphylococcus, Burkholderia, Ochrobactrum, Enterobacter* and *Stenotrophomonas* exhibit antagonistic potential (Tariq et al. 2017). This antagonistic potential is evident from the fact that many plant beneficial microorganisms secrete lytic enzyme to hydrolyze compounds like, hemicellulose, chitin and protein to hamper the activities of pathogens including the lysis of fungal cell wall (Neeraja et al. 2010). *Serratia marcescens* reduce the mycelial growth of soil borne pathogen, *Sclerotium rolfsii* through overexpression of chitinases (Ordentlich et al. 1988). Moreover, during this cell wall degradation dead organic matter and plant residues are also decomposed for carbon supplies. Similarly, Lysobacter controls *Pythium* and *Bipolaris* fungal species through glucanase and these enzymes also reduce the plant biotic stresses by directly parasitizing the phytopathogens (Palumbo et al. 2005; Haran et al. 1996). Apart from these cell wall degrading enzymes, certain PGPRs strains (e.g. *Enterobacter cloacae, Azospirillum brasilense, Bacillus, Rhizobium, Pseudomonas etc.*) contain 1-aminocyclopropane-1-carboxylate (ACC) deaminase enzyme which regulates the production of gaseous hormone, ethylene in plants. In fact, this enzyme hydrolyzes the ethylene precursor, ACC in to ammonia and ketobutyrate thereby inhibiting the ethylene production under stressed environments including flooding, drought, salinity heavy metals. ACC-deaminase containing PGPRs relieve the plants against such stresses and improve plant growth and development (Saleem et al. 2007).

6 Application of Microbes as Bio Pesticides/Bio Control Agents

Agricultural productivity remains under threat due to biotic factors such as plant pathogens. Currently, these plant pathogens are being controlled through chemical method i.e. pesticides/fungicides application. Although this method is effective and convenient but it has proven to be a potential threat to environment and all life forms on earth. Hence, the use of biological method i.e. microbial inoculants is environment friendly as well as sustainable approach for profitable agricultural productivity (Shafi et al. 2017). *Bacillus* and *Pseudomonas* spp. are two PGPR that have been reported to be effective bio-control agents (Gong et al. 2006; Leonardo et al. 2006).

Among these bacterial species, *Bacillus subtilis, Bacillus amyloliquefaciens*, and *Bacillus cereus* are the most effective species at controlling plant diseases through various mechanisms (Francis et al. 2010). *Bacillus* spp. have the ability to form spores which allows these PGPR to survive in a wide range of environmental conditions, thus facilitating the effective formulation of biofertilizer (Perez-Garcia et al. 2011). Bacillus-based biocontrol agents are playing a significant role in biopesticide industry. Shafi et al. (2017) also reported that most of the *Bacillus* sp. are very effective against multiple types of plant pathogens. These biocontrol agents have the ability to combat disease causing soil borne pathogens by using a variety of mechanisms. Production of antimicrobial compounds (lipopeptides, antibiotics), competition for nutrients and space and induction of host resistance (induced systemic resistance) are the major mode of actions employed by these bacteria.

One of the most effective modes of action of rhizobacteria in suppression of soil borne pathogens is *Antibiosis* (Handelsman and Stab 1996). Fungal plant pathogens are inhibited by several groups of antibiotics produced by biocontrol agents inoculated to most of the crops (Haas and Defago 2005). Soilborne infections of cereal crops like wheat, rice, maize, chickpea, and barley are suppressed by antibiotics produced by these biocontrol agents (Raaijmakers et al. 1999).

Pseudomonas fluorescens, P. putida, *P. aeruginosa, Bacillus subtilis* and other *Bacillus* spp. are most effective PGPR with market potential as Bio pesticides. The PGPR isolates are prepared by using different inert carrier materials and fermented in solid or liquid forms and marketed in packets or bottles (Fig. 4). The method of application of bacterial inoculants may be seed treatment, bio-priming, seedling dip, soil application, foliar spray, fruit spray, hive insert, sucker treatment and sett treatment. Application of PGPR inoculants in a consortium is more effective as compare to single strain inoculants for inhibition or suppression of soilborne plant pathogens and for better plant growth (Ji et al. 2006). Efficacy of antagonists can be

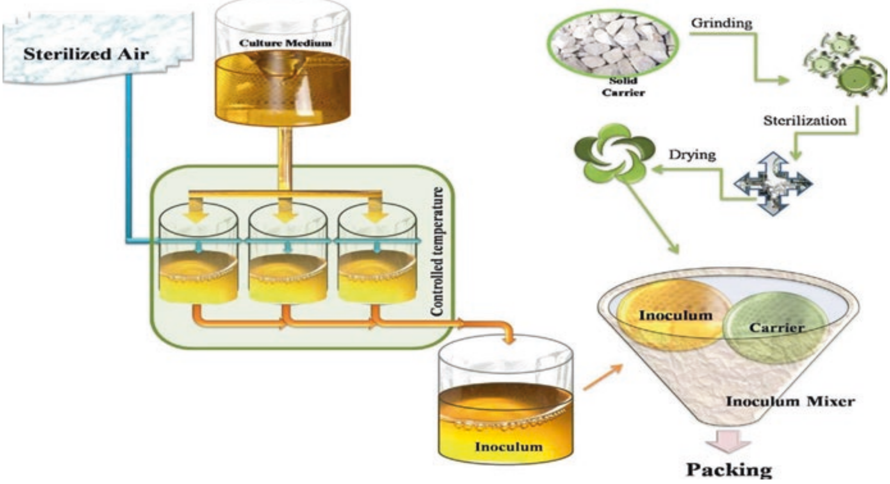

Fig. 4 A generalized sketch of the biofertilizer/bio-pesticide preparation by industry where PGPRs are preserved in an appropriate carrier molecule and packaged for commercial application at farmer's end. (Adapted from Tabassum et al. 2017)

improved by supplementation of chitin in the formulation. These inocula are being commercialized in many countries including; India, China, Japan, Germany, Australia, USA. In North America for example, more than 33 products of beneficial rhizobacteria are commercially available for their application in field or greenhouse. It is important to mention that some PGPRs are potential threats to human beings for example *Pseudomonas aeruginosa, P. cepacia* and *Bacillus cereus.* Hence, careful measures must be taken before their large-scale application for pest and disease management (Nakkeeran et al. 2005). The commercialized bio pesticides available in international market are listed in Table 3.

7 Application of Microbes as Bio Remediators of Contaminated Soils

Many microorganisms impart synergistic effects on plants through improving plant growth, accumulating heavy metals, reducing the toxicities of heavy metals and mitigating the effects of other environmental and edaphic factors such as; drought, over wetting, temperature extremes, climate change stresses and salinity. For example, plant growth promoting rhizobacteria used as biofertilizer also intensify the phytoremediation process (Sobariu et al. 2017).

Over the last many decades, heavy metals (HMs) have posed serious threats to both plants and animals. Moreover, HMs have devastatingly compromised the food safety and security via food chain contamination, soil degradation, stunted plant growth and hampering microbial community (Ashraf et al. 2017). Empirical evidences indicate that certain bacterial species enhance the accumulation of heavy metal in plants along with promoting plant growth (Asad et al. 2018). These microorganisms in fact are capable to degrade inorganic pollutants through transformation, rhizo- degradation and volatilization (Ullah et al. 2015). Physiology behind metal detoxification may include metal complexation, impermeability of metals and enzymatic detoxification (Pavel et al. 2013). Apart from these mechanisms, plant beneficial microbes possess metal resistant genes to detoxify different metal and metalloids. Under heavy metal stress several genes are induced in these microorganisms to detoxify heavy metals and metalloids such as; Zn^{+2}, Cu^{+2}, Cd^{+2}, Ni^{+2} and Hg^{+2} (Ullah et al. 2015). For example, transcriptome analysis of *Brassica* and model plant *Arabidopsis thaliana* indicated the involvement of transcription factors (TFs), bZIP, bHLH and AP2/ERF under heavy metal stress (Singh et al. 2016). Several target proteins to detoxify heavy metals in *A. thaliana*, *Zea mays* and *Oryza sativa* have been discovered. Moreover, several metabolites such as phenols, amino acids, organic acids and glutathione have also been reported to alleviate the metal stresses in plants (Singh et al. 2016). The over expression of stress responsive transcription factors (e.g. bZIP) were reported to be mediated by PGPR in *Arabidopsis* and Chickpea (Tiwari et al. 2017). Similarly, phytohormones (SA, ABA, ethylene and JA) released by plant beneficial microorganisms have also been reported to be involved to alleviate the heavy metal stressed plants. Perhaps induction of stress signaling genes in the presence of plant beneficial microorganisms elucidates a complex interaction between microorganism, plant and HMs in stress response and tolerance which warrants further investigations to understand this complex network of interactions between plants and microbes under metal stress (Tiwari and Lata 2018).

The microbial populations in heavy metal contaminated environment mostly belong to notable genera, *pseudomonas*, *Arthrobacter*, *Bacillus* and *Rhizobia* (Pires et al. 2017). Many of the plant growth promoting attributes i.e. nitrogen fixation and nitrogenase activities are very sensitive to heavy metals stresses but resistant strains of these microorganisms have been noted to carry out these activities successfully at contaminated sites. According to Checcucci et al. (2017) symbiotic relationship between rhizobia and legume are well researched for heavy metal detoxification and improving quality of contaminated sites. Amongst fungal genera, *Basidiomycota, Ascomycota* and *arbuscular mycorrhiza* have been reported to reduce heavy metal toxicity and improve the degraded soil quality (Narendrula-Kotha and Nkongolo 2017). In fact, these functions are primarily accomplished by binding of heavy metal ions on the cell surface or transporting in to the cell and changing the metal toxicity and deterioration in soil (Gadd 2010). However, metal-microbe interactions are very complex and success rate very much depends on physico-chemical properties of soil, concentration of HM in soil and microbial composition.

8 Microbial Applications as Abiotic Stress Ameliorators

Microbial inoculants are being investigated for their potential as ameliorators of following abiotic stresses.

8.1 Drought Stress

Drought is one of the major limitations toward reduced agricultural productivity in both arid and semi-arid habitats. Drought affects nitrogen fixation and major constraint for reduced legumes production (Serraj 2009). In legumes, drought is equally detrimental for nitrogen fixation during pre and post nodule formation; during post nodule formation drought causes reduced root development. The water content of rhizosphere is a potent factor determining the nutrients and oxygen supplies to plants and microorganisms (Gestel et al. 1993). These interactions among microorganisms, water and plant roots in fact formulate the soil structure which is a key determinant of soil health and hence crop productivity. For example, soil moisture levels administer the production and consumption of protein and polysaccharides by the bacteria thereby influencing the soil structure (Roberson and Firestone 1992). Similarly, exopolysaccharides released by microbes bind soil particles forming macro and micro aggregates having greater or less than 250 μm diameter respectively (Oades 1993) and hence helping plant roots to creep through these aggregates. Moisture stress may alter the biological and physico-chemical properties of soil rendering it unfit for soil biodiversity and agricultural productivity. Bacterial species such as *Pseudomonas* and *Azospirillum* commonly used as biofertilizers successfully survive under stressed environments because of exopolysaccharides (EPS) which enhance water retention and regulate carbon sources. Therefore, it becomes imperative to manage the moisture stressed or drought affected soils for meeting the food demands and use of PGPRs could provide a sustainable option for managing such soils. EPS producing microorganisms based applications may bridge this gap thereby alleviating the stressed plants and enhance productivity. A study conducted by Sandhya et al. (2009) on sunflower inoculated with *Pseudomonas putida* strain GAP-P45 revealed that almost one third of the microbial isolates used in the study could tolerate drought stress up to a level of −0.73 Mpa. The most exciting part of the investigation was that EPS production of studied strains was more prominent under stressed conditions and it continued to increase with increasing stress. Moreover, these strains expressed growth promoting properties through production of several metabolites including; HCN, phosphate solubilization, ammonia, IAA and GA production under water limiting conditions which is pre-requisite for sustainable agricultural productivity under limited water availability. Arbuscular mycorrhiza (AM) fungi have been reported to rescue plants from drought stress. Under water limiting conditions, AM increase the nitrogen availability (Bowles et al. 2018) This is perhaps because; under drought conditions these fungi absorb water more efficiently due to alterations in root architecture or most probably due to regulation of abscisic acid concentration under drought conditions (Khalvati et al. 2005; Jahromi et al. 2008). Hyphae of AM fungi penetrate deeply in to the soil in the thirst of acquiring more water and nutrients and also improve soil structure, the key factor for enhanced productivity of crops. Enhanced growth and yield of several important fruit crops (Peach, apple, citrus) is observed through AM fungi colonization (Nunes et al. 2010)

8.2 Salinity Stress

Salinity disturbs the uptake of mineral nutrients and their distribution within plant body. Moreover, it negatively influences the plant metabolism consequently reduce the quality and quantity of agricultural productivity (Silveira et al. 2003). Reduced water content of plants and creating drought like conditions, significant decline in uptake of essential nutrients, decreased photosynthetic rates, reduced biomass of plant is all attributed to the salinity stress in plants (Ben-Asher et al. 2006). Salinity has also been reported to cause abnormalities in the soil biodiversity and many genera of plant beneficial microbes have disappeared from the saline environments (Andronov et al. 2012). However, many microbial species still survive in such toxic ecologies. For example, several microbial species such as *Rhizobia*, *Azospirillum* and *Bacillus* are able to survive under such environments but exhibit varying abilities to tolerate salinity (Lloret et al. 1995). All these bacterial species are well researched for their plant growth promotion, N_2 fixation, disease suppression and plant growth hormones production characteristics (Naz et al. 2009). Ethylene production is aggravated in response to salinity resulting in stunted root growth. Madhaiyan et al. (2007) while studying the effects of exogenous application of ACC (1-aminocyclopropane-1-carboxylic acid) in *Brassica campestris* observed enhanced level of ethylene and stunted root growth in treated plants compared with control. Plant growth promoting rhizobacteria (PGPR) enhance plant growth under salinity stress conditions, which is possibly because of production of ACC-deaminase to hydrolyze ethylene precursor. So perhaps use of PGPRs is one of the plausible options to reduce salinity induced ethylene production (Mayak et al. 1999). Ethylene production in plants is enhanced in response to biotic and abiotic stresses, however PGPRs applications inhibited ethylene production significantly under these stresses, indicating the involvement of PGPRs in plant management under stressed environments (Ahmad et al. 2011). PGPR exhibit the characteristic to maintain an equilibrium in ionic concentration thereby increasing the growth and yield of crops due to reduced ethylene production (Nadeem et al. 2009). Different bacterial strains have varying potential for propagating the ACC-deaminase activity, most probably because other growth promoting activities including phosphate solubilization, production of lytic enzyme, chitinase activity, N_2 fixation are also continued along with ACC-deaminase activity (Nadeem et al. 2009; Ahmad et al. 2011). Under saline environments, a higher K^+/Na^+ ratio is very important which increases the plant tolerance against salinity (Hamdia et al. 2004). Many plant growth promoting bacteria are capable to help plants tolerate exceeded level of Na^+ by secreting exopolysaccharides (EPS) which reduce the level of Na^+ uptake (Nadeem et al. 2014) through biofilm formation (Qurashi and Sabri 2012). Interestingly, these exopolysaccharides also help plants to withstand water limiting environments and protect the microorganisms against drought stress (Sandhya et al. 2009).

8.3 Climate Change Stress

Agriculture and the linked food security are largely dependent on the natural environment, hence facing critical threats from climate change. Combination of abiotic and biotic stresses have multiplied the risks for sustainable crop production particularly in the sub-tropical regions around the world. Extreme weather events including drought, floods, torrential rains, increasing temperatures has certainly jeopardized the regional as well as global food security with considerable shifts in cropping pattern and the associated reduced yields of major agricultural crops. For example, South Asia being the hotspot of climate change has witnessed significant reductions in paddy and wheat yields because of increasing temperature, less rain followed by increasing water stresses influenced by climate change. Abiotic stresses including temperature, salinity, drought cause approximately 50% yield losses in agricultural productivity (Kaur et al. 2018). Evolving and adapting cost effective and sustainable technologies for sustainable crop production under extreme environments has always been a challenge. A plethora of literature exists detailing the technologies for adapting to the changing climate scenarios whereby developing drought resistant varieties and resource management among others have proved to be very effective in combating climate change stresses (Venkateswarlu and Shanker 2009). Use of microorganisms for promoting plant growth, controlling pathogens/diseases and nutrient management under climate change stresses has attracted plausible attention of research community (Grover et al. 2011). These microorganisms reside in the plant rhizosphere and thereof transmit several direct and indirect benefits to the plant (Saxena et al. 2005). Major microbial genera capable to induce tolerance in plants exposed to climate change stresses include; *Bacillus*, *Pseudomonas*, *Rhizobium*, *Paenibacillus*, *Azospirillum*, *Burkholderia*, *Achromobacter*, *Enterobacter*, *Methylobacterium* and *Microbacterium*. These microorganisms protect the plants against frost, higher temperature, over wetting, drought and other climate change stresses (Grover et al. 2011). Therefore, using these microorganisms to alleviate the agricultural crops could be an effective technology for enhancing the agricultural productivity on sustainable basis.

Although, mechanisms for alleviating the plants against climate change abnormalities are under researched and warrants further investigation. However, production of auxins, gibberellins and root exudates to increase the growth and surface area of roots to quench and uptake more nutrients by microorganisms is considered as one possible explanation of helping plants withstand the abiotic stresses including climate change (Egamberdieva and Kucharova 2009). For example, PGPR have been found to be involved in rescuing the vegetable and oil seed crops against many abiotic stresses (Barassi et al. 2006). Similarly, inoculation of *Paenibacillus* and *Azospirillum brasilense* in *Arabidopsis* and wheat respectively, relieved the plants against drought stress which helped the plants to maintain better water status and minerals Ca, Mg and K (Timmusk and Wagner 1999). A study conducted by Mayak et al. (2004) involving inoculation of tomato with *Achromobacter piechaudii* induced systemic resistance against drought in inoculated plants as compared to control.

The role of stress hormone ‘ethylene’ is widely known to reduce root/shoot growth under stress conditions. ACC-deaminase producing bacteria including *Rhizobia*, *Pseudomonas* degrade the plant ACC and enhance nitrogen and energy supply to plants. Glick (2007) noted that these bacterial strains lessen the abnormalities caused by ethylene. Hence, role of ACC-deaminase producing PGPR is pivotal for agriculture management under stressed environments as these microbes induce longer roots enhancing water uptake efficiency of plants under water limiting conditions (Zahir et al. 2008). Arbuscular mycorrhiza (AM) fungi have also been reported for rescuing the stressed plants. This AM fungi induced stress resistance is mediated by several enzymes such as peroxidase (POD), superoxide dismutase (SOD), catalase (CAT) and abscisic acid (ABA). During abiotic stress, activities of these enzymes were enhanced by AM fungi which improved the osmotic

Fig. 5 Example of suppression of *Pythium ultimum* root rot in 4-week-old sorghum seedlings by bacterial strains isolated from the rhizosphere of wild grasses in South Africa. (**a**) Plants inoculated with *P. ultimum* and treated with rhizobacterial isolates. (**b**) Control plants that were treated only with *P. ultimum* developed visible root rot and necrotic leaves. (Adapted from Idris et al. 2007)

adjustment thereby increasing the drought resistance in citrus seedlings (Wu et al. 2005). Similarly, lavender plants inoculated with mycorrhizae possessed better water, N and K contents and exhibited greater biomass than uninoculated plants under drought stress (Marulanda et al. 2007). Growth hormone, ABA is also suggested behind AM fungi reduced drought resistance in plants (Aroca et al. 2008). Extreme flood events have deleterious effects on crops causing irreparable losses to the peasants and altering the socioeconomic balance in the affected areas. In wetlands, AM fungi are well established and alleviate the submerged crops after flooding events. *Glomus intraradices* colonization of *Pterocarpus officinalis* seedlings substantially improved resistance of inoculated plants through improved P uptake (Fougnies et al. 2007). Resistance against flooding is also mediated by enhanced proline content and osmotic adjustment in submerged plants as observed by Neto et al. (2006). Abiotic and biotic stresses triggered by rapidly changing climate scenarios, environmental and edaphic factors pose serious challenges for sustainable agriculture and use of beneficial plant microbes such as; PGPRs and AM fungi could prove to be an effective, environment friendly option for sustainable and enhanced agricultural productivity under compromised environments (Fig. 5).

9 Conclusions and Future Research

Scientific literature and research on presence/survival of beneficial rhizobacteria in rhizosphere, illustrations of specified mode of action, characterization of plant beneficial traits and evaluation of inoculants in pot and field trials has revealed that PGPR has proved to be potential candidates for sustainable agricultural development. Applications of beneficial rhizobacteria (microbial inoculants) as biofertilizers and bio pesticides has been successful to make a reasonable space in international market. Bio pesticide/Biocontrol agents (BCAs) have shown more consistency in market as compared to biofertilizers. Application of microbial inoculants for bioremediation of heavy metals/pollutants and abiotic stress amelioration is catching attention of scientific community however practical application of these techniques is limited and is a matter of future scope of this technology. Microbial inoculants have limited acceptance perhaps because of the complications during field application, their sensitivity toward environmental changes and most importantly lack of farmer's awareness. To cope with these challenges there is a dire need of comprehensive integrated agricultural management policy. Integration of these renewable resources with those of non-renewable ones in a wise way could lead to a sustainable agriculture system.

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