

Chapter 10

Consortium of Plant-Growth-Promoting Bacteria: Future Perspective in Agriculture

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10.1 Dynamics of Bacterial Diversity in Rhizosphere

Soil is a dynamic, living matrix that is an essential part of the terrestrial ecosystem. It is a critical resource not only for agricultural production and food security but also toward maintenance of most life processes, and it is considered as a storehouse of microbial activity. In 1904, Hiltner coined the term “rhizosphere” referring area around the close vicinity of plant root in which bacteria are abundantly present, most often organized in microcolonies. To exploit the positive effects in rhizosphere, beneficial microorganisms are isolated from soil, cultured, and inoculated into soil (Glick 1995). These rhizobacteria utilize nutrients secreted by the plant root, and in return they influence plant growth in direct or indirect ways including increasing nitrogen uptake, synthesis of phytohormones (auxin, cytokinin), solubilization of minerals, and iron chelation (Bowen and Rovira 1999). These organisms also may suppress soilborne pathogens by producing siderophores, antimicrobial metabolites, or by competing for nutrients and/or niches (Nelson 2004). All of these

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activities result in stimulation of plant growth, henceforth yield. Therefore such rhizobacteria are commonly referred as “plant-growth-promoting rhizobacteria” (PGPR) (Kloepper and Schroth 1978). In fact, use of PGPR in modern agriculture is considered as excellent eco-friendly biotechnological approach to replace harmful chemicals.

In intensive cropping system, supplementing soil nutrients by the use of chemical fertilizer is considered inevitable for obtaining optimum yield of crops. However, their utilization efficiency remains low, due to loss by volatilization, denitrification, leaching, and conversion into unavailable forms. Now it is well established that continuous use of chemical fertilizers subverts the soil ecology, disrupts environment, degrades soil fertility, and consequently shows harmful effects on human health (Ayala and Rao 2002) and also contaminates ground water (Joshi et al. 2006). Therefore, large-scale application of PGPR to crops as inoculants would be attractive as it would substantially reduce the use of chemical fertilizers and pesticides, which often pollute the environment. In addition, the application of PGPR would increase crop yield, thereby helping to feed the growing world population to ensure food security to all. A growing number of PGPR are being marketed (Bashan 1998; Pinton et al. 2001).

Recently, there has been a shift in the approach of workers, as, instead of using a single strain of plant-growth-promoting rhizobacterium as inoculants, nowadays co-inoculation of two or multiple PGPR is experimented to achieve prominent multifarious effect on productivity for improving sustainable agriculture system. Seneviratne (2003) recognized that co-inoculation and co-culture of microbes perform the tasks better than the individual microbes. However, in recent years, many studies have shown that co-inoculation of rhizobia and some plant-growth-promoting bacteria (PGPB) increases nodulation and growth in a wide variety of legumes (Bullied et al. 2002; Shaharoon et al. 2006; Tilak et al. 2006). Earlier, microbial studies performed without plants indicated that some combinations allow the bacteria to interact with each other synergistically, provide nutrients, remove inhibitory products, and stimulate each other through physical and biochemical activities that may enhance some beneficial aspects of their physiology (Bashan 1998). When the two different strains are made into an inoculum consortium, each of the individual strains of the consortium not only outcompetes with the others for rhizospheric establishments but also complements functionally for plant growth promotion (Shenoy and Kalagudi 2003). Combined use of plant-growth-promoting rhizobacteria is based on the principles of natural ecosystems, sustained by their constituents. In other terms, the quality and quantity of inhabitants and specific ecological parameters, *i.e.*, the greater the diversity and number of inhabitants, the higher the order of their interaction and more stable the ecosystem. This concept of combined use of plant-growth-promoting rhizobacteria is an effort to shift microbiological equilibrium in favor of increased plant growth production, nutrient uptake, and protection (Higa 1991; Parr et al. 1994). The various strategies that may be used for consortium formulation are summarized in Fig. 10.1.

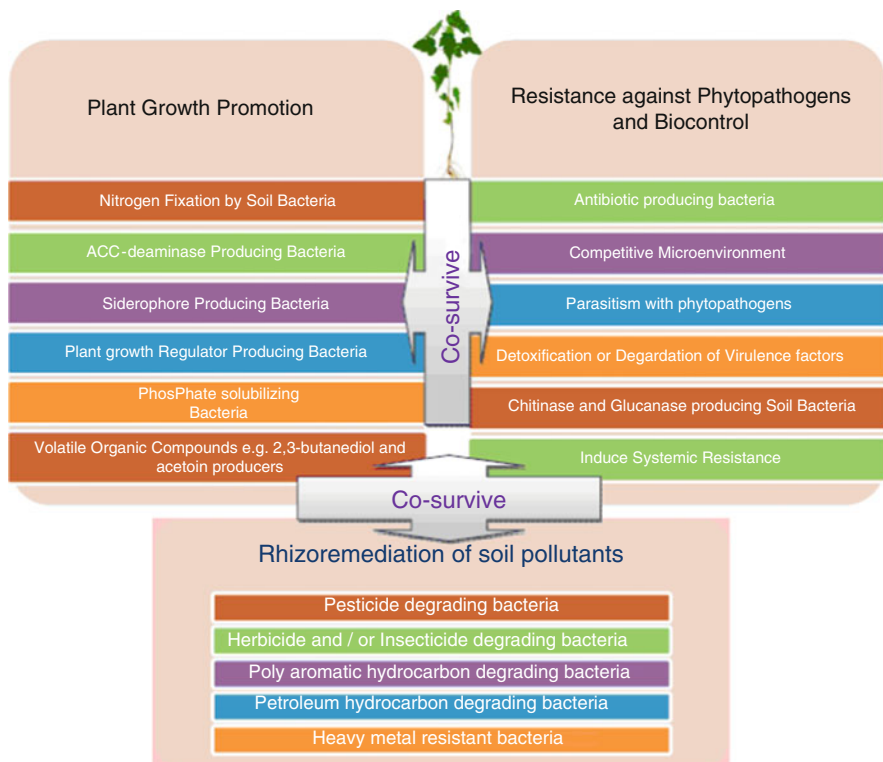


Fig. 10.1 The strategy of rhizobacteria consortium formulation may be designed to enhance the desired benefits. On one hand, diversity attributed for plant growth promotion may be accumulated in finished products of consortium, and/or properties for resistance against soilborne pathogen can be included. Additional benefits including bioremediation can also be achieved. The properties of rhizospheric competence and cosurvival of participating strains are prerequisite for effective formulation

10.2 Consortia of Rhizobia and PGPR

Legume root is colonized by numerous rhizospheric microorganisms, and these organisms have definite influence on the survival and nodulation ability of seed-inoculated rhizobia (Dashti et al. 1998; Davison 1988). There have been several reports where association of bacterial genera with wild legume or other plants improved plant yield, plant health, and nodulation (Bai et al. 2002a, 2003; Zakhia et al. 2006; Rajendran et al. 2008). Some PGPR strains enhance legume growth, nodulation, and nitrogen fixation when coinoculated with rhizobia. Examples of these are *Azospirillum* (Groppa et al. 1998), *Azotobacter* (Burns et al. 1981), *Bacillus* (Srinivasan et al. 1996), *Pseudomonas* (Grimes and Mount 1984), *Serratia* (Chanway et al. 1989; Zhang et al. 1996), and *Streptomyces* (Li and Alexander 1988). *Azotobacter* sp. is known to promote nodulation when used as coinoculum with many different

P-solubilizing organisms including *Bacillus* species (Sahin et al. 2004; Cakmakci et al. 2001). Co-inoculation of P-solubilizing bacteria and *Rhizobium* stimulated plant growth more profoundly than their separate inoculations (Perveen et al. 2002) while there is positive interaction of *Rhizobium* with P-solubilizing sp. of *Bacillus* has translated into significant yield increases of legumes (Zaidi et al. 2003). Increase in nodulation and yield components of legume crops following inoculation with N₂-fixing and P-solubilizing microbes has also been reported by other researchers (Garcia et al. 2004; Gupta 2004). Toro et al. (1998) reported that inoculation of phosphate-solubilizing bacteria (PSB) enhanced nodulation and N₂ fixation by alfalfa plants, in parallel with an increase in the P content of plant tissues, and concluded that an improvement in P nutrition of the plant resulting from the presence of PSB was responsible for increased nodulation and N₂ fixation, as it is well known that these processes are P dependent (Barea et al. 2005).

Dashti et al. (1998) and Dubey (1996) observed that nodule number and nodule weight increase as a result of co-inoculation with *Bradyrhizobium japonicum* and PGPR, for two cultivars of soybean, as compared to inoculation of the *B. japonicum* alone. In co-inoculation studies with PGPR and *Rhizobium/Bradyrhizobium* spp., an increase in the root and shoot weight, plant vigor, nitrogen fixation, and grain yield has been shown in various other legumes such as common bean (Grimes and Mount 1984) and green gram (Sindhu et al. 1999). Sindhu et al. (1999) reported increase in nodule number, nodule fresh weight, plant dry weight, and total plant N uptake when *Bradyrhizobium* sp. (*Vigna*) was coinoculated with *Pseudomonas* isolates. Combined inoculation of *Rhizobium* sp. with *Pseudomonas striata* or *Bacillus polymyxa* and *Bacillus megaterium* has shown significant increase in dry weight, grain yield, and phosphorus uptake over the uninoculated control in legumes (Elkoca et al. 2008). Yadegari et al. (2008) also showed that co-inoculation of PGPR with *Rhizobium* sp. and *Bradyrhizobium* sp. increases the root and shoot weight, plant vigor, and grain yield in various legumes. Additionally, Marisa and coworker also demonstrated the co-inoculation with *S. meliloti* strain 3DOh13 and *P. aurantiaca* SR1 on alfalfa plant which resulted in increase in the fresh and dry shoots and root weight of plant. Sindhu et al. (2002) showed that the effect of *Pseudomonas* strain MRS13 isolated from the rhizosphere of green gram on coinoculation with *Mesorhizobium* sp. *cicer* strain Ca181 in legumes, particularly chickpea, indicated the increased in dry weight ratios, i.e., 1.92, 1.84, and 1.98, of plant, as compared to uninoculated control. Similar results were obtained by Sindhu et al. (2002) with co-inoculation of *Pseudomonas* strain and *Mesorhizobium* which stimulated nodule fresh weight and plant dry weight. Co-inoculation studies with PGPR and *Bradyrhizobium japonicum* have also demonstrated increase in root and shoot weight, seed yield, plant vigor, nodulation, and nitrogen fixation in soybean plants (Li and Alexander 1988). An increase in grain yield, nodule dry matter, and nitrogenase activity was also obtained in chickpea inoculated with a mixture of *Aspersion brasilense* and *Rhizobium* strains (Rai 1983).

Grimes and Mount (1984) found that a *Pseudomonas putida* strain (M17), which had been selected as a potential biological control agent, markedly increased *Rhizobium* nodulation of bean in field soils. Polonenko et al. (1987) found similar

effects of certain rhizobacteria (primarily fluorescent pseudomonads) on nodulation of soybean roots by *B. japonicum*. Numerous studies have therefore indicated that co-inoculation of *Bradyrhizobium* and certain PGPR can positively affect symbiotic nitrogen fixation by enhancing both root nodule number or mass (Polonenko et al. 1987) and increasing nitrogenase activity (Alagawadi and Gaur 1988). Zhang et al. (1996) demonstrated that co-inoculation of *B. japonicum* with *S. proteamaculans* 1-102 reduced the decrease in nitrogen concentration of plant shoots at 15°C root zone temperatures, and further, there was no difference for plant shoot nitrogen content between 15°C and 17°C ± 5°C root zone temperatures. Bai et al. (2002b) showed that co-inoculation of *Serratia proteamaculans* 1-102 and *S. liquefaciens* 2-68 with *Bradyrhizobium japonicum* on soybean [*Glycine max* (L.) Merr.] resulted in significant increased in growth, nodulation, and nitrogen fixation under controlled root zone temperatures (RZTs; 25°C, 20°C, and 15°C) in soilless media.

Actinomycetes have also been reported to improve rhizobial symbiosis in legumes. Solans et al. (2009) observed that the symbiotic effect of saprophytic actinomycetes and *Sinorhizobium meliloti* results in promotion of nodulation in *Medicago sativa* in the presence of high nitrogen. Solans et al. (2011) assayed the effect of co-inoculation of saprophytic rhizoactinomycetes *Streptomyces* MM40, *Actinoplanes* ME3, and *Micromonospora* MM18 isolated from the root nodule surface of the nitrogen-fixing actinorhizal plant *Discaria trinervis* with *Sinorhizobium meliloti* 2011 on *Medicago sativa* in fertilized soil with a low level of N (0.07 mM). The inoculation of the actinomycetes alone did not show any effect on plant growth. Meanwhile, when actinomycetes were coinoculated with *S. meliloti*, nodulation and plant growth were significantly stimulated compared to plants inoculated with only *S. meliloti*. The analysis of nodulation kinetics of simultaneous or delayed co-inoculations suggests that the effect of the actinomycetes operates in early infection and nodule development, counteracting the autoregulation of nodulation by the plant, and the reason for this stimulation is because the actinomycete was found in the symbiotic nitrogen-fixing state of the plant.

Fuhrmann and Wollum (1989) reported that co-inoculation of siderophore-producing pseudomonads with mixtures of the competing bradyrhizobia typically enhanced nodulation by *B. japonicum* strain USDA 110. Srinivasan et al. (1996) found that IAA-producing *Bacillus* isolates promoted root growth and/or nodulation when coinoculated with *Rhizobium elti* TAL 182 on *Phaseolus vulgaris* and also recorded increased nodule number, nodule fresh weight, nitrogenase activity, leghemoglobin content, and total soluble protein content in the root nodules of *P. vulgaris*.

In some instances, some endophytic genera are known to improve also the symbiosis *B. subtilis* NEB4 and NEB5 and *B. thuringiensis* NEB17 as endophytes of nodules of soybean were found to enhance growth and nodulation in greenhouse and field when coinoculated with *B. japonicum*, by providing consistent increases in nodule number, nodule weight, shoot weight, root weight, total biomass, total nitrogen, and grain yield (Bai et al. 2003). Recently, Tilak and Reddy (2006) reported increase in the yield of pigeon pea due to bacterization with endophytic *B. cereus* and *B. circulans* isolated from maize rhizosphere. However, the yield was relatively low, as compared to the treatment of these isolates in maize and wheat, possibly due to the differential response of PGPR with *Rhizobium* population in soil.

Chebotar et al. (2001) demonstrated that some plant growth regulators of *Pseudomonas* strains, but not all, increased nodule number and acetylene reduction in soybean plants inoculated with *B. japonicum*. Recently, Mañero et al. (2003) observed effect of culture filtrates of PGPR on growth, germination, and biological nitrogen fixation by lupin seedling. Role of metabolites other than phytohormones, such as siderophores, phytoalexins, and flavonoids, in enhancement of nodule formation has also been proposed (Lucas-Garcia et al. 2004), but this hypothesis has not been verified.

10.3 Consortium Comprising Free-Living PGPR

Plant growth promotion activity has been reported for strains belonging to many different genera such as *Azoarcus*, *Azospirillum*, *Azotobacter*, *Arthrobacter*, *Bacillus*, *Clostridium*, *Enterobacter*, *Gluconoacetobacter*, *Pseudomonas*, and *Serratia* (Somers et al. 2004; Roy et al. 2009). Veen et al. (1997) critically reviewed the reasons for poor performance of agricultural bioinocula in natural environments and in the rhizosphere of host plants and suggested that, instead of using a single strain, for a single trait, use of multiple microbial consortia for multiple benefits can also thrive together in unique ecological niches in ideal proportions. In fact, Pratibha et al. (2011) reported several PGPR in tea rhizosphere including *Rhizobium*, *Burkholderia*, *Azotobacter*, etc., from tea garden soil of south Assam, India. Significant increase in seedling growth because of mixed culture of *Pseudomonas* and *Bacillus* on wheat under field experiments is well documented (van Elsas 1986). Inoculation with *Azospirillum halopraeferens*, a mixture of two *Azospirillum brasilense* strains and a mixture of *Bacillus licheniformis* and *Phyllobacterium* sp., has significantly increased plant height and dry weight of oilseed (*Salicornia bigelovii*) (Bashan et al. 2000). Recently, Mahmood et al. (2010) reported the influence of various rhizobacteria sp. and *Agrobacteria* sp. inoculation, singly and combined on biochemical and physiological changes of the important banana plantlets in Malaysia, Berangan cultivar (AAA). Amutha et al. (2009) studied coaggregation of *Azospirillum brasilense* with other PGPR cells using different cations and to evaluate bioinoculation effect of *Azospirillum* coaggregates on the plant height, grain yield, number of panicles, productive tillers (%), plant dry weight, and nitrogen content of rice. Dual inoculation *Azospirillum* sp. and *Azotobacter* sp. resulted in increase in total “N” content of rice and significant stimulation of their populations in rhizosphere and also increased the plant growth; concentrations of indoleacetic acid (IAA), P, Mg, and N; and total soluble sugars in wheat seedlings and shoots (Elshanshoury 1995). Similarly, it was reported that co-inoculation of two PGPR, i.e., *Enterobacter* sp. and *Pseudomonas* sp., resulted in better survival of these strains as compared to individual (Neyra et al. 1995). In an interesting report, three unrelated bacteria—methylophilic *Methylobacterium oryzae* along with *Azospirillum brasilense* and *Burkholderia pyrrocinia*—were reported to have positive effect on nutrient uptake and therefore, the growth of tomato, red pepper, and rice plants (Aronen et al. 2002; Madhaiyan et al. 2010). Similarly, presence of *S. meliloti*

PP3, *R. leguminosorum* Pcc, and *Bacillus* sp. B1 did not have any detrimental effect on viability of PGPR strain—*Burkholderia* sp. MSSP, in wheat bran-based multispecies consortium (Pandey and Maheshwari 2007).

10.4 Consortium of Rhizobacteria in Bioremediation

Soil microbial communities are also used for biological treatment of environmental pollutants which involves the breakdown of contamination into nontoxic forms using microbiological processes (Lee et al. 1998). The advantages of employing mixed cultures as opposed to pure cultures in bioremediation have been widely demonstrated because of the synergistic interactions among members of the association. The mechanism by which isolates with bioremediation potential get benefit from synergistic interactions is considered to be complex. Yet it is possible that one species removes the toxic metabolites (that otherwise may hinder microbial activities) of the species preceding it while it is also possible that the second species are able to degrade compounds that the first are able to only partially (Alexander 1999). Rambeloarisoa et al. (1984) reported that a consortium of eight strains (comprising members of six genera) is able to effectively degrading crude oil than individual strain. Interestingly, only five of these strains were able to grow in pure cultures using hydrocarbons as sole source of C. However, when the other three strains were removed from the consortium, the effectiveness of the mixed culture was remarkably reduced. These further support the theory that each member in a microbial community has a significant role and may need to depend on the presence of other species or strains to be able to survive. Nikolopoulou et al. (2007) reported that the maximum degradation of n-alkanes (C₈–C₁₁) is achieved in treatments where bacterial consortium of *Acinetobacter* sp. T4 was applied along with *Pseudomonas putida* PB4.

10.5 AM Fungi and PGPR: Mycorrhizosphere Interaction

Arbuscular mycorrhiza fungi (AMF) are known to affect plant growth and health by improving mineral nutrition (Clark and Zeto 2000) and by increasing resistance to, or tolerance of, biotic (Cordier et al. 1996; Trotta et al. 1996) and abiotic stress (Ordookhani et al. 2010). So, the co-inoculation of AM fungi with PGPR strain provides a significant stimulation of microbial density and activity in soil. Synergistic interactions between AMF and symbiotic N₂-fixing bacteria such as *Azotobacter chroococcum*, *Azospirillum* spp., and *Acetobacter diazotrophicus* have been reported by many researchers (Suresh and Bagyaraj 2002). Similarly, in another study, Muthukumar and Udaiyan (2006) reported the application of AM fungi and plant-growth-promoting rhizobacteria co-inoculation on the growth of bamboo plant in tropical soil with and without fertilizer.

Both AMF and PGPR complement each other in their role in N fixation, phytohormone production, P solubilization, and increasing surface absorption. Multifaceted interactions of AM fungi with various microorganisms and microfauna in the mycorrhizosphere may be positive or negative. Inoculation of tomato roots with PGPR (*Pseudomonas putida* strain, *Azotobacter chroococcum*, and *Azosprillum lipoferum*) and AMF (*Glomus intradices* + *Glomus mossea* + *Glomus etunicatum*) has been reported to improve the quality of tomato fruit (Ordookhani et al. 2010). The positive synergistic interactions between mycorrhizosphere AM fungi and various N-fixing and P-solubilizing bacteria are the basis of application of these microbes as biofertilizer and bioprotectant agents (Bansal et al. 2002). These microbes are regulated by AMF for their own benefit, which in turn benefit the host plant. Meyer and Linderman (1986) reported enhanced mycorrhization of clover in the presence of PGPR rhizobacterium *Pseudomonas putida*. Similar observations were made later by several other researchers (Suresh and Bagyaraj 2002). All these studies suggest that colonization of plant roots by AM fungi significantly influences the mycorrhizosphere microorganisms, including PGPR. Requena et al. (1997) observed the selective and specific functional compatibility relationships in plant response between arbuscular mycorrhizal (AM) fungi, *Glomus coronatum*, native, and *Glomus intraradices*, exotic, two *Rhizobium* bacteria (NR4 and NR9, both native), and two PGPR (A2, native, and E, exotic) were screened for effectiveness by a single-inoculation trial in soil microcosms in *Anthyllis cytisoides* L., a mycotrophic pioneer legume, dominant in the target mediterranean ecosystem. A further screening for the appropriate double and triple combinations of microbial inoculants was then performed, and the parameters evaluated were biomass accumulation and allocation, N and P uptake, N₂ fixation (¹⁵N), or root system quality. Overall, *G. coronatum*, native in the field site, was more effective than the exotic *G. intraradices* in co-inoculation treatments. In general, their results support the importance of physiological and genetic adaptation of microbes to the whole environment.

10.6 Enhanced Biocontrol Activity by Application of Consortium

Most of the research up till now is focused on biocontrol agents that are applied singly. Nevertheless, a single biocontrol agent is less likely to be active in all kinds of soil environment and agricultural ecosystems (Raupach and Kloepper 1998; de Boer et al. 2003) and also may result in inadequate colonization, limited tolerance to change in environment conditions, and fluctuation in production of antifungal metabolites as suggested (Weller and Thomashao 1994; Dowling and O’Gara 1994; Fukui et al. 1999). Prudent application of binary or multiple mixtures of PGPR inoculants can expand the spectrum of biocontrol activity (Felici et al. 2008). The production of hydrogen cyanide (HCN) and 2, 4-diacetylphloroglucinol (DAPG) is

a major factor in the control of soilborne diseases by *Pseudomonas fluorescens* CHA0. Co-inoculation of strain CHA0 with DAPG-producing *P. fluorescens* biocontrol strains Pf-68 and Pf-100 did result in neither a substantial alteration of *hcnA* nor *phlA* expression in CHA0 on bean roots (Jamali et al. 2009).

Consortium of PGPR is also known to improve induced systemic resistance (ISR) in host plants. Consortium and coaggregate application of *P. fluorescens* (PF-3) and *Paenibacillus polymyxa* (B-19), together with challenge inoculation of *Pyricularia oryzae* on the enhancement of ISR in rice-*Pyricularia oryzae* pathosystem, was studied under pot culture condition with rice cv.ASD-19. The application of PGPR cells, as coaggregates, was found to augment the total phenol content and defense enzyme activities such as PO and PPO content of rice plant to a higher level (Umashankari and Sekar 2011).

Though use of consortia or mixtures of two or more microbial strains to enhance the level of antagonistic substances and consistency in disease control is considered as good approach (Raupach and Kloepper 1998; Fukui et al. 1999; de Boer et al. 2003), however, proper strategy for effective screening and selection of desired strains for consortium formulation is still desirable (Walsh et al. 2001). It was found that many of the potential strains strongly inhibited others and vice versa in the in vitro assay. Similarly, some bacterial isolates showing promising attributes for plant growth promotion, like *Bacillus* sp. B7, *Pseudomonas* sp. L2, and *Rhizobium* sp. Pb, failed to survive in the presence of other potential PGPR. Earlier, inhibitory activity of pseudomonads on the other rhizobacteria has been reported by Pierson and Weller (1994).

10.7 Effect on Growth Physiology of PGPR in Mixed Inoculations

The growth physiology of various strains incorporated in mixed species consortium is an important aspect, which is sometimes ignored. The growth rate may affect the stability of artificial microbial ecosystem, in process of establishment by the application of consortium. Large difference in growth rate may result in a condition where slow growing strain gets outnumbered by fast growing partner. This imbalance may affect the colonizing abilities, affecting the plant growth.

In one study, it was found that growth of *Burkholderia* sp. MSSP was similar in monospecies and mixed species cultures with *S. meliloti* PP3. However, 25% increase in mean growth rate was recorded for *S. meliloti* PP3 when grown in mixed species of two species culture with respect to monoculture. The authors hypothesized that association with *Burkholderia* sp. favors *S. meliloti* as an adaptation of high rate of reproduction—a well-known evolved strategy that enable organisms to successfully survive and maintain themselves in communities as also explained by Andrews (1991). Derylo and Skorupska (1993) observed synergistic effect of *Pseudomonas* sp. 267 on growth of *R. leguminosarum* bv. *trifoli* 24 significantly. Shanmungam et al. (2002) cocultured *P. fluorescens* and *Rhizobium* sp. in vitro and reported positive

interaction between them. However, growth profile was measured by viable count, depending solely on their morphological characteristics.

Coimmobilization of the freshwater microalga *Chlorella vulgaris* and the plant-growth-promoting bacterium *Azospirillum brasilense* in small alginate beads resulted in a significantly increased growth of the microalga. Dry and fresh weight, total number of cells, size of the microalgal clusters (colonies) within the bead, number of microalgal cells per cluster, and the levels of microalgal pigments significantly increased (Gonzalez and Bashan 2000).

10.8 Concept and Potential of Bacterial Consortium in Future

Though the challenge of formulating a multifunctional microbial inoculum by adding appropriate microbial combinations for biotechnological approach to improve plant growth requires matching efforts, yet, with this multipurpose consortium, it can be tailored to help plants to establish, grow well, and survive in nutrient-deficient, stressful conditions.

Numerous recent studies showed a promising trend in the field of inoculation technology. Mixed inoculants (combinations of microorganisms) that interact synergistically are currently being devised. An example of this is *Azospirillum*, one of the most studied bacteria that associate with plants (Bashan and Holguin 1997a). It may associate with sugar- or polysaccharide-degrading bacteria (PDB), establishing a metabolic association where the sugar-degrading bacteria produce degradation and fermentation products used by *Azospirillum* as a carbon source, which in turn provides polysaccharide-degrading bacteria (PDB) with nitrogen. Other examples are the association between *Azospirillum* and *Bacillus* that degrades pectin, *Azospirillum* and *Cellulomonas* that degrades cellulose, and *Azospirillum* and *Emerobacter cloacae* that ferments glucose (Halsall 1993; Kaiser 1995).

Plant studies have also shown that the beneficial effects of *Azospirillum* on plants can be enhanced by co-inoculation with other microorganisms which frequently increased growth and yield of plant, compared to single inoculation; provided the plants with more balanced nutrition; and improved absorption of nitrogen, phosphorus, and mineral nutrients (Bashan and Holguin 1997a,b). Thus, plant growth can be increased by dual inoculation with *Azospirillum* and phosphate-solubilizing bacteria (Belimov et al. 1995). *Azospirillum* is also considered to be a *Rhizobium* “helper” by its stimulating nodulation, nodule activity, and plant metabolism and resistance to unfavorable conditions (Fabbri and Del Gallo 1995; Itzigsohn et al. 1993). Other successful combinations include *Azospirillum* or *Azotobacter* mixed with *Streptomyces* (Elshanshoury 1995) and *Azospirillum* with the fungal biocontrol agent *Phialophora radicola* (Flouri et al. 1995). Mixed inoculation with diazotrophic bacteria and arbuscular mycorrhizal fungi creates synergistic interactions that may result in a significant increase in growth, in the phosphorus content in plants, enhanced mycorrhizal infection, and an enhancement in the uptake of mineral nutrients such as phosphorus, nitrogen, zinc, copper, and iron

(Barea 1997; Chanway and Holl 1991; Garbaye 1994; Gori and Favilli 1995; Isopi et al. 1995; Linderman 1992; Linderman and Paulitz 1990; Rozycki et al. 1994; Singh et al. 1990).

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