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Bacterial Endophytes in Sustainable Crop Production: Applications, Recent Developments and Challenges Ahead

Dr. Swaroopa Marella

Division of Zoology, Department of Sericulture,

Sri Padmavathi Mahila Visva Vidyalayam, Tirupati-517502, Andhra Pradesh, India

Abstract: **One of the effective ways of developing sustainable agriculture to ensure human and animal food production with a minimal disturbance to the environment is the exploration of Microbe-based symbioses in plants. Developing molecular approaches based on the continuity of microbial pools which are circulating regularly between soil-, plant- and animal-provided niches in natural and agricultural ecosystems serves in the effectual management of symbiotic microbial communities. Analysis of this circulation could enable the creation of highly productive microbe-based sustainable agricultural system, while attending the ecological and genetic consequences of the broad application of microbes in agricultural practice. Also simulation of evolution implemented in the mutualistic symbioses aid in enhancing ecological efficiency, functional integrity and genotypic specificity ensuing 'applied co-evolutionary research' addressing the ecological and molecular mechanisms for mutual adaptation and parallel speciation of plant and microbial partner. The use of microbial symbiotic signals or their derivatives for remodeling plant developmental or defensive functions may be depicted as a promising field. Yet agricultural microbiology confronts several significant ecological and genetic challenges imposed by the broad application of symbiotic microbes. Some of these challenges are being associated with opportunistic or even regular human pathogens. However the prospects for a future development of agricultural microbiology may involve the construction of novel multipartite endo- and ecto-symbiotic communities based on extended genetic and molecular (metagenomic) analyses.**

Keywords: **Plant–Microbial Symbioses, Agricultural Microbiology, Sustainable Agriculture, Agronomic Potential, Ecological Impacts.**

I. INTRODUCTION

There exist a complex network of interactions of plants with microorganisms; some of these may be beneficial, while others are detrimental, but the beneficial microorganisms are by far the largest and still widely unexplored part. There is an ever growing demand worldwide for implanting ecologically compatible and environmentally friendly techniques in agriculture, capable of providing adequate sustenance for the increasing human population and for improving the quality and quantity of certain agricultural products. For these reasons, the application of beneficial microorganisms proves to be an important alternative to some of the traditional agricultural practices which have in practice for long and very often severely alter the agro-ecosystem balance and cause serious damage to health. This review aims to highlight the status and implications of application of beneficial microbes that provide an option for future prospects in sustainable agriculture.

Plant-micro-organism interactions

Microorganisms of the soil interact with plant roots and soil constituents at the root-soil interface, where root exudates and decaying plant material is rich source of carbon compounds for the heterotrophic biota (Barea et al., 2005; Bisseling et al., 2009). The number of bacteria in the rhizosphere (the narrow region of soil that is directly influenced by root secretions and associated soil microorganisms) and rhizoplane (the external surface of roots together with closely adhering soil particles and debris) is always higher than in the soil devoid of plants because soils devoid of plants lack substances secreted from the roots of plants, like for example; as soon as a seed starts to germinate, a relatively large amount of carbon and nitrogen compounds i.e., sugars, organic acid, amino acids, and vitamins are excreted into the surrounding environment that attracts a large population of microorganisms inducing vigorous competition between the different species (Okon, 1994). Moreover, rhizosphere microbiomes typically differ between plant species (Bisseling et al., 2009).

There are several modes by which microorganisms can be beneficial to plant health, which can be related either to an indirect or a direct positive effect. Beneficial microorganisms are known to be biocontrol agents and/or growth promoters. Microorganisms have indirect positive effects on plants, affecting adversely the population density, dynamics and metabolic activities of soil-borne pathogens, mainly through competition, antibiosis, lysis and hyperparasitism. Competitive colonization of the rhizosphere and successful establishment in the root zone is a prerequisite for effective biocontrol. Antagonistic microorganisms often produce a range of different antimicrobial secondary metabolites, and/or extracellular lytic enzymes. For example hyperparasitism *in Trichoderma*; involves secretion of chitinases and cellulases, contact with the pathogen, coiling of hyphae around the hyphae of the pathogen, enzymatic digestion of its cell wall and penetration.

Direct positive effects on plants by rhizosphere microorganisms involve production of phytohormones, non-symbiotic nitrogen fixation, and the increase of availability of phosphate and other nutrients in the soil through phytostimulation and biofertilization of plants (Burdman et al., 2000). Numerous compounds such as HCN, phenazines, pyrrolnitrin, and pyoluteorin as well as, enzymes, antibiotics, metabolites and phytohormones that are toxic to pathogens and phenomena such as quorum sensing and chemotaxis, are vital for rhizosphere colonization (Castro-Sowinski et al., 2007; Ramette et al., 2011; Jousset et al., 2011). Under iron-limiting conditions habitats of soil and plant surfaces, can produce low molecular weight compounds called siderophores, that sequester iron in a competitive way, thus depriving pathogenic fungi of this essential and often scarcely bioavailable element (Pedraza et al., 2007).

Many rhizosphere microorganisms can activate plant defence mechanisms and induce a systemic response in plants. Inoculation with non-pathogenic root zone bacteria can trigger signalling pathways that lead to higher pathogen resistance of the host, called induced systemic resistance (ISR). Several of the bacteria that are well documented for beneficial effects under abiotic stress conditions, such as *Bacillus* sp., have been shown to induce ISR (Chakraborty et al., 2006). Some beneficial rhizosphere microbes can elicit physical or chemical changes related to plant defense, a process often referred to as ISR, and/or tolerance to abiotic stress, such as drought, salt or nutrient excess or deficiency. The term “induced systemic tolerance” (IST) has been proposed for the latter PGPR-induced changes in plants. IST relates to an enhanced tolerance to abiotic stresses (Yang et al., 2009). The metabolic pathways for signal transduction in plant defense responses can intercommunicate with other plant stress responses. In addition, the genes that are involved in plant responses to biotic and abiotic stresses can be co-regulated (Dimkpa et al., 2009).

Role of Bacterial endophytes in Sustainable Crop Production

Agriculture is the oldest economic sector in the world, and is more dependent on fertile soils and a stable climate than any other trade. At the same time, it has a huge influence on the ecological balance, water and soil quality, and on the preservation of biological diversity. Since the middle of the last century, agricultural techniques and economic framework conditions worldwide have undergone such a radical transformation that agriculture has become a major source of environmental pollution. The investigation about ecologically compatible techniques in agriculture and environmental sciences can take essential advantage from the use of beneficial microorganisms as plant-microbe interactions fulfill important ecosystem functions.

Plant diseases are a major cause of yield losses and ecosystem instability worldwide. Use of agrochemicals to protect crop against plant pathogens has been increasing along with the intensification of agricultural production over the last few decades. Chemical fertilizers increase yield in agriculture but are expensive and harm the environment. They deplete non-renewable energy via side effects, such as leaching out, and polluting water basins, destroying micro-organisms and friendly insects, making the crop more susceptible to the attack of diseases, reducing soil fertility, thereby causing irreparable damage to the overall system.

To feed the burgeoning population of the world, farmers heavily rely on the use of chemical fertilizers especially inorganic nitrogen. Application of inorganic fertilizer has many repercussions, as it leads to ground and surface water contamination due to leaching and denitrification, which is detrimental for human and animal health. Secondly, manufacturing of industrial nitrogen fertilizer uses non-renewable resources like natural gas and coal and causes production of green house gases viz., CO_2 and NO_2 contributing to global warming (Bhattacharjee et al., 2008). Therefore, it's high time to opt for alternative fertilizers which can be used in sustainable agricultural practices without affecting the environment. Application of plant growth promoting associative bacteria can be a potential option for enhancing growth and yield of plant in sustainable manner.

On the basis of area of colonization, Plant Associated Bacteria (PAB) can be grouped into associative bacteria that include rhizospheric (in vicinity of root) and rhizoplanic (on surface of root) bacteria and, endophytic bacteria. Term 'endophytic bacteria' is referred to those bacteria, which colonizes in the interior of the plant parts, viz, root, stem or seeds without causing any harmful effect on host plant (Hallmann et al., 1997). These bacteria may promote plant growth in terms of increased germination rates, biomass, leaf area, chlorophyll content, nitrogen content, protein content, hydraulic activity, roots and shoot length, yield and tolerance to abiotic stresses like draught, flood, salinity etc. PAB can promote plant growth directly through Biological Nitrogen Fixation (BNF), phytohormone production, phosphate solubilization, inhibition of ethylene biosynthesis in response to biotic or abiotic stress (induced systemic tolerance) etc., or indirectly through inducing resistance to pathogen (Bhattacharya and Jha, 2012). Present review aims to focus on plant growth promoting abilities of rhizospheric and endophytic bacteria and their molecular aspects. PAB has been classified as the plant growth promoting bacteria on the basis of basic mechanisms through which it stimulates plant growth as PGPB, which induces plant growth directly and; bio-controller, which protects plants by inhibiting growth of pathogen and/or insect (Backman and Sikora, 2008).

Based on the properties, associative/endophytic bacteria have been classified as Plant Growth Promoting Bacteria (PGPB) and biocontrol bacteria. PGPB may benefit associated plants through providing nutrition (nitrogen, phosphorous and iron), production of plant hormone and may enable plant tolerate abiotic stressors. Biocontrol bacteria protect plants from invasion of pathogenic microorganisms through antagonism and/or induced systemic resistance.

Plant Growth Promoting Bacteria:

Associative bacteria as well as endophytic bacteria use same mechanisms to influence plant growth. However, they differ in efficiency through which they exert their beneficial effect. Based on various properties, plant growth promoting bacteria can be classified as biofertilizers, rhizoremediators, phytostimulators and stress controllers. Bacterial fertilizer is referred to the bacteria that supply nutrition to the associated plant. They may benefit plants by providing utilizable nitrogen through fixation of atmospheric nitrogen or they make free phosphate available from insoluble source of phosphate. Plant growth promotion due to solubilization of zinc compound driven by Gluconoacetobacter has also been reported (Lugtenberg and Kamilova, 2009).

The use of PGPR could be a better alternative to chemical fertilizers. They are economical, not harmful to the environment and could easily be found. PGPR are free-living bacteria of beneficial importance to agriculture and abound in the rhizosphere, the region around the root. Some PGPR have more than one mechanism of accomplishing increased plant growth, such as the production of enzymes, bioactive factors, antibiotics, metabolites as well as growth promoters. The mechanisms of action presented are not an all-encompassing list. Although variability in field performance is common, PGPR are environmentally friendly, unlike the overuse of chemical fertilizers.

Plant Growth-Promoting Rhizobacteria (PGPR) are non-pathogenic, strongly root colonizing bacteria on the surface of plant's roots which increase plant's yield by one or more mechanisms. PGPR bioactive factors are substances that impact on growth. Examples are root exudates, vitamins, and amino acids. By the Production of phytohormones that contribute to the host root respiration rate, metabolism and root abundance and hence improved the mineral and water uptake in inoculated plants. By regulating ethylene production in roots, through producing metabolites like Hydrogen cyanide (HCN), 2,4-diacetylphloroglucinol (DAPG) and siderophores are antifungal compounds that assists in the control of soil-borne diseases. By Diacetylphloroglucinol (DAPG) production - DAPG is a polyketide antibiotic that suppresses a wide variety of soil-borne fungal pathogens, through release of enzymes for the Fixation of N2 that is transferred to the plant, through Organic and inorganic phosphate solubilization, by Production of exo-enzymes like chitinase, cellulase, b-1,3-glucanase, protease, lipase that suppress deleterious microbes.

PGPR present encourage beneficial effects on plant health and growth, suppress disease-causing microbes and accelerate nutrient availability and assimilation. Thus, in the quest to improve soil fertility and crop yield and to reduce the negative impacts of chemical fertilizers on the environment, there is a need to exploit PGPR for continued beneficial agricultural purposes. PGPR exist in the rhizosphere and this is defined as the region around the root. Seed inoculation with PGPR could be by drench application, seed bacterization, or via dual treatment. PGPR compensate for the reduction in plant growth caused by weed infestation (Babalola et al. 2007b), drought stress (Zahir et al. 2008), heavy metals (Kumar et al. 2009), salt stress (Egamberdieva 2008; Kaymak et al. 2009) and some other unfavorable environmental conditions. One of the mechanisms by which bacteria are adsorbed onto soil particles is by simple ion exchange and a soil is said to be naturally fertile when the soil organisms are releasing inorganic nutrients from the organic reserves at a rate sufficient to sustain rapid plant growth. These bacteria belong to the genera Acetobacter, Acinetobacter, Alcaligenes, Arthrobacter, Azoarcus, Azospirillum, Azotobacter, Bacillus, Beijerinckia, Burkholderia, Derxia, Enterobacter, Gluconacetobacter, Herbaspirillum, Klebsiella, Ochrobactrum, Pantoae, Pseudomonas, Rhodococcus, Serratia, Stenotrophomonas and Zoogloea and have been subject of extensive research throughout the years.

Microbial Ecology, Biotechnology and Sustainable Agriculture

Now the development of sustainable agriculture is being widely promoted in which the increased productivity of plants and animals is ensured using their natural adaptive potentials, with a minimal disturbance of the environment (Noble & Ruaysoongnern, 2010). It is popular opinion that the most promising strategy to reach this goal is to substitute hazardous use of mineral fertilizers, pesticides in agriculture with environment-friendly symbiotic microbes, which could improve the nutrition of crops, as well as their protection against biotic (pathogens, pests) and abiotic (including pollution and climatic change) challenges (Yang et al., 2009).

The effect of the growth promotion exerted by PGPRs is mainly related to the release of metabolites and nitrogen fixation processes, the provision of bioavailable phosphorus for plant uptake, sequestration of iron by siderophores, production of plant hormones like auxins, cytochinins and gibberellins, and lowering of plant ethylene levels (Glick, 1995; Glick et al.,1999; Tortora et al., 2011). On the contrary, biocontrol occurs through an indirect action of the BCAs that interact with soil pathogens through several mechanisms such as antibiosis (production of antimicrobial compounds), competition for iron and nutrients or for colonization sites, predation and parasitism, induction of resistance factors (for example the plant is strongly stimulated to synthesize substance called phytoalexins, small molecules with antibiotic activity, which can inhibit the growth of many pathogenic microorganisms), production of enzymes such as chitinase, glucanase, protease and lipase (Whipps, 2001).

The beneficial bacteria are widely studied by microbiologists and agronomists because of their potential in increasing plant production (Somers et al., 2004). The research involving the use of PGPRs were made mainly on herbaceous plants in open field environments and in horticultural crops. Moreover, their application has recently expanded both in forestry and in phytoremediation of contaminated soils. Strains belonging to the genera *Azospirillum* (Okon & Labandera-Gonzalez, 1994; Okon & Itzigshon, 1995; Dobbelaere et al., 2001), *Bacillus* (Reddy & Rahe, 1989; Kokalis-Bourelle et al., 2002; Kokalis-Burelle et al., 2006) and *Pseudomonas* (McCullaugh et al., 1996; Meyer et al., 2010) have been used in experimental tests on a wide range of economically important crops.

Growth promotion and biocontrol can be due to the same microorganism that positively influences the development of the plant through different mechanisms, for instance the increased availability and assimilation of the mineral nutritional components, the release of growth factors and the suppression of pathogenic microorganisms. This is translated in more resistant and healthy plants. In addition, PGPR species are able to metabolize numerous and varying carbon sources, to multiply quickly and above all to show a greater competence in colonizing the rhizosphere in comparison to deleterious microorganisms.

Endophytic bacteria, that dwell intercellularly in association with plants for most, if not all, of their life cycles (Bacon & Hinton, 2007), have been used for biological control of various plant diseases, as well as for enhanced plant agronomic characteristics, such as increased drought tolerance and nitrogen efficiency. These bacteria, that include anaerobic, aerobic, and microaerobic species, live within the intercellular spaces of plant, where they feed on apoplastic nutrients, as non-pathogens. They can be found within a wide variety of plant tissue, including seeds, fruit, stems, roots and tubers (Surette et al., 2003). Among them are comprised bacterial diazotrophs that do not form nodules on hosts, such as *Azospirillum* species, and some *Rhizobium* species. Isolated from a large diversity of plants (Rosenblueth & Martínez-Romero, 2006), in general they occur at lower population density than rizospheric bacteria or bacterial pathogens and can positively affect host plant growth (Long et al., 2008). What makes bacterial endophytes suitable as biocontrol agents is their colonization of an ecological niche similar to that of phytopathogens (Ryan et al., 2008).

Endophytes can be strictly dependent on the host plant for their growth and survival ("obligate endophytes"); alternatively, "facultative endophytes" have a stage in their life cycle in which they exist outside host plants (Hardoim et al., 2008). The latter group probably comprises the vast majority of the microorganisms that can thrive inside plants. These endophytes often originate from the soil, initially infecting the host plant by colonizing, for instance, the cracks formed in lateral root junctions and then quickly spreading to the intercellular spaces in the root. Hence, to be ecologically successful, endophytes that infect plants from soil must be competent root colonizers. Endophytic colonization of the plant interior is presumably similar, at least in the initial phases, to colonization of plant roots by rhizobacteria. Competitive rhizosphere bacteria, for example members of the genera *Pseudomonas* (e.g. *P. fluorescens*), *Azospirillum* (e.g. *A. brasilense*) and *Bacillus* (Pedraza et al.,2007; Mano & Morisaki, 2008), are often also found as colonizers of the internal tissue of plants.

A suite of environmental and genetic factors is presumed to have a role in enabling a specific bacterium to become endophytic. Inside the plant tissues, modulation of plant physiology by tinkering with the plant ethylene levels has emerged as a major strategy, because any effect on this plant stress signal has major impacts on the bacterial niche. How bacteria modulate plant ethylene concentrations is the key to their ecological success or competence as endophytes. The concept of "competent endophytes" has been proposed as a way to characterize those bacteria that possess key genetic machinery required to colonize the endosphere and to persist in it. This is in contrast to "opportunistic endophytes", which are competent rhizosphere colonizers that might become endophytic by coincidentally entering root tissue, but lack genes that are a key to their ecological success inside the plant. Moreover, it is possible to distinguish "passenger endophytes" that, in the absence of any machinery for efficient root colonization or entry, might enter plants purely as a result of chance events (Rosenblueth & Martínez-Romero, 2006; Mercado-Blanco & Bakker, 2007). Bacterial endophytes, used for biological control of various plant diseases and for improved plant agronomic characteristics, as they have the advantage of being relatively protected from the competitive soil environment; moreover, they usually grow in the same plant tissue where bacterial plant pathogens are detected (Bulgari et al., 2009): so far, they have been shown to promote growth in potatoes, tomatoes, and rice, and they have been shown to be capable of inducing both biotic and abiotic stress resistance (Surette et al., 2003). A large number of mechanisms are being proposed to explain this effect: production of antimicrobial compounds, macronutrient competition, siderophore production, induced systemic resistance. This array of proposed mechanisms reflects the high diversity of endophytic bacteria.

II. APPLICATIONS

Application of associative bacteria for sustainable agriculture holds immense potential. These bacteria are known to enhance growth and yield of plants by fixing atmospheric nitrogen, solubilization of phosphate, production of phytohormones and siderophores, possession of antagonistic activity as well as reducing the level of stress ethylene in host plants. Colonization of these bacteria can be tracked by tagging them with certain molecular markers such as β-glucuronidase (gus) or green fluorescent protein (gfp) followed by electron microscopy or laser scanning confocal microscopy. Associative bacteria and endophytes may express genes differentially to colonize and establish the plant interior. They may also use 'quorum sensing' molecules for colonization process.

The major impact of agricultural microbiology on sustainable agriculture would be to substitute agrochemicals (mineral fertilizers, pesticides) with microbial preparations. However, this substitution is usually partial and only sometimes may be complete, e.g. in recently domesticated leguminous crops, which retain a high potential for symbiotrophic N nutrition, typical for many wild legumes (Provorov & Tikhonovich, 2003). The application of nutritional symbionts could be based on plant mixotrophy, e.g. on a simultaneous symbiotrophic and combined N nutrition. This is why the maximal productivity of the majority of crops is reached using an optimal (species- and genotype-specific) combination of both nutritional types because of which a high sustainability of legume production may be achieved (Provorov et al., 1998). Moreover, the energy costs for N_2 fixation and for assimilation of combined N differ by less than 10% (Andrews et al., 2009). The balance between symbiotrophic and combined N nutrition may be improved by a rapid removal of N-compounds from the actively N_2-fixing symbioses, as has been suggested for tropical forest ecosystems (Hedin et al., 2009).

Though exploitation of beneficial soil – borne microorganims is mostly oriented to improve plant growth and protection in an agricultural context, nevertheless several applications in a wider environmental sense has been reported in literature. *Pseudomonas fluorescent* (Russo et al., 1996; 2001; 2005), *Bacillus subtilis* (Felici et al., 2008), *Rhizobium* spp (Toffanin et al., 2000; Casella et al., 2006), are some of beneficial bacteria applied in experimental/scientific work as biofertilizers and/or biocontrol agents in agriculture. Other potential applications currently include micropropagation, bioremediation and phytoremediation, phosphate solubilization, soil aggregation, sewage treatment, bioleaching, oil recovery, coal scrubbing and biogas production.

III. CHALLENGES

At the moment, as a consequence of (i) a growing interest towards low input agriculture systems (organic farming, biodinamics, natural farming), (ii) a favourable opinion of consumers for food with no chemicals, and (iii) the increased difficulties in the employment of chemicals according to the most recent laws, "microbiological revolution" is being promoted, and the use of microorganisms in agriculture is increasing. Despite the huge potentiality of beneficial microorganisms, a relative low diffusion need to be highlighted, owing to "inconsistent" results in field experiments, and also owing to prejudices derived from the easy and large availability of chemicals.

The use of beneficial soil microorganisms as agricultural inputs for improved crop production requires the selection of rhizosphere-competent microorganisms with plant growth-promoting attributes (Hynes et al. 2008). The beneficial bacteria termed PGPR are disease-suppressive microorganisms that improve plant health. Findings and documentation abound, and all point towards the need to commercially exploit PGPR as biofertilizers for their agricultural benefits. From a general perspective, however, the problems of variability in colonization efficiency, field performance and rhizosphere competence are controversial issues.

Further development of agricultural microbiology faces several important ecological and genetic challenges imposed by the broad application of symbiotic microbes. Some of these challenges are associated with opportunistic or even regular human pathogens, which are frequently found in endophytic communities, including Bacillus, Burkholderia, Enterobacter, Escherichia, Klebsiella, Salmonella and Staphylococcus species (Ryan et al., 2008).

Despite the fact that a large number of associative and endophytic bacteria have shown plant growth promoting properties at laboratory and green house level, these bacteria fail to exhibit consistent performance under natural conditions. For instance, the factors that affect colonization and thus PGPB derived benefit to plant are many like soil type, nutritional status of soil, host plant genotype and age as well as climatic conditions (Bhattacharya and Jha, 2012). High amount of available utilizable nitrogen reduces colonization of PGPB in natural condition and it may also reduce the process of nitrogen fixation due to regulatory mechanism acting in the diazotrophic isolates. Therefore, a challenge is posed for systematic optimization for the application of suitable PGPB isolates and the amount of fertilizer to be added to obtain maximum output.

Prominent among the major challenges includes selection of plant genotype and age, and compatible associative bacteria. Understanding of this compatibility would help to enhance productivity by using specific strain for inoculation. Since, the colonization of associative bacteria also depends upon seasonal changes and soil hydric stress, multiples field trials are required to optimize parameters for obtaining the maximum output. Another factor which is to be addressed in detail is the plant defense response which may limit or reduce the colonization of associative bacteria. In addition, colonization mechanism is still not well understood. Indepth analysis of genomic and functional genomics studies can help manipulate the conditions to enhance colonization process and increased plant growth properties. Lastly, extensive and intensive research on the understanding of associative and endophytic ecology will be major determinant to maximize benefit from these bacteria.

IV. FUTURE POTENTIAL

The agronomic potential of plant–microbial symbioses proceeds from the analysis of their ecological impacts, which have been best studied for N_2 fixing (Franche et al., 2009). The broad application of microbes in sustainable agriculture is due to the genetic dependency of plants on the beneficial functions provided by symbiotic cohabitants (Noble & Ruaysoongnern, 2010). This analyses is based on 'applied co-evolutionary research' (Arnold et al., 2010), addressing the ecological and molecular mechanisms for mutual adaptation and parallel speciation of plant and microbial partners. For plant–fungal interactions, it has been demonstrated that the host genotype represents the leading factor in the biogeographic distribution of mycobionts and for their evolution within the mutualist↔antagonist and specialist↔generalist continua (Peay et al., 2010).

This approach is most promising in legume–rhizobia symbioses where the strong correlations between the ecological efficiency of mutualism and its genotypic specificity are evident (Provorov & Vorobyov, 2010b). At present, a wide spectrum of preparations of diverse microbial species may be used to enhance crop production (Andrews et al., 2010). However, different approaches for improving the nutritional and defensive types of microbial mutualists need to be developed. For the nutritional types, an effective colonisation of plants in a host-specific manner is optimal and the impacts of beneficial symbionts are increased in parallel with their host specificity (Provorov & Vorobyov, 2009). The application of microbial symbiotic signals or their derivatives for remodelling plant developmental or defensive functions may represent a promising field for agricultural biotechnology.

The prospects for a future development of agricultural microbiology may involve the construction of novel multipartite endo- and ecto-symbiotic communities based on extended genetic and molecular (metagenomic) analyses. The primary approach for such construction is to create composite inoculants, which simulate the natural plant-associated microbial communities. For balancing the host plant metabolism, a combination of N- and P-providing symbionts would appear promising, including the endosymbiotic rhizobia + VAM-fungi (Shtark et al., 2010),

V. CONCLUSIONS

Agricultural microbiology is the present paramount research field responsible for the transfer of knowledge from general microbiology and microbial ecology to the agricultural biotechnologies. The present review focussed on plants and emphasized the importance of micro-organisms in relation to agriculture (Wang et al., 2009) and to the biocontrol of phytopathogens (Mohammed et al., 2008) and plant growth promotion.

An increased knowledge of microbe-based symbioses in plants can provide effective ways of developing sustainable agriculture in order to ensure human and animal food production with a minimal disturbance of the environment. The effective management of symbiotic microbial communities is possible using molecular approaches based on the continuity of microbial pools which are circulating regularly between soil-, plant- and animal-provided niches in natural and agricultural ecosystems (Kupriyanov et al., 2010), analysis of this circulation could enable the creation of highly productive microbe-based sustainable agricultural system, while addressing the ecological and genetic consequences of the broad application of microbes in agricultural practice.

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