Chapter 5
The Impact of Mycorrhizosphere Bacterial Communities on Soil Biofunctioning in Tropical and Mediterranean Forest Ecosystems

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5.1 Introduction

Mycorrhizal fungi constitute a key functional group of soil biota that greatly contribute to productivity and sustainability of terrestrial ecosystems. These are ubiquitous components of most of the ecosystems throughout the world and are considered key ecological factors in governing the cycles of major plant nutrients and in sustaining the vegetation cover (van der Hejden et al. 1998; Requena et al. 2001; Schreiner et al. 2003). Two major forms of mycorrhizae are usually recognized: the arbuscular mycorrhiza (AM) and the ectomycorrhizas (ECMs). AM symbiosis is the most widespread mycorrhizal association type with plants that have true roots, i.e. pteridophytes, gymnosperms and angiosperms (Read et al. 2000).

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They affect about 80–90% land plants in natural, agricultural and forest ecosystems (Brundrett 2002). ECMs are found with trees and shrubs, gymnosperms (Pinaceae) and angiosperms, and usually result from the association of homobasidiomycetes with about 20 families of mainly woody plants (Smith and Read 2008). These woody species are associated with a larger (compared to the AM symbiosis) diversity of fungi, comprising 4,000–6,000 species, mainly Basidiomycetes and Ascomycetes (Allen et al. 1995; Valentine et al. 2004). The benefits of mycorrhizal symbiosis to the host plant have usually been considered as a result of closed relationships between the host plant and the fungal symbiont. However, the hyphae of these symbiotic fungi provide an increased area for interactions with other soil microorganisms by enhancing the development of the host plant root systems.

Plant roots influence the soil microbial community in the narrow zone of soil called the rhizosphere (Hiltner 1904). In the rhizosphere, root exudates and organic breakdown products provide a specific ecological niche for microbes with chemical and physical characteristics (concentration and forms of nutrients, soil structure, moisture and pH) that differ from those recorded in the bulk soil (Timonen and Marschner 2006). Hence the density and activity of microorganisms are generally higher in the rhizosphere than in the bulk soil (Lynch 1990). Since plant roots in natural conditions are mycorrhizal and it is well known that the fungal symbiosis modifies root functions, microbial communities associated with mycorrhizas differ from those of the non-mycorrhizal plants and of the surrounding soil (Garbaye 1991; Garbaye and Bowen 1987, 1989). Hence the rhizosphere concept has been enlarged to include the fungal component of the symbiosis to give the term "mycorrhizosphere" (Rambelli 1973; Linderman 1988). The mycorrhizosphere is the zone influenced by both the root and the mycorrhizal fungus. It includes the soil surrounding individual fungal hyphae that has been named "hyphosphere" (Johansson et al. 2004). Mycorrhizal fungi act as a bridge connecting the rhizosphere to the bulk soil and, through an active development of extraradical mycelium into the soil, the mycorrhizosphere extends root–fungal interactions with soil microbial communities (Whipps 2004; Leake et al. 2004). Interactions within the mycorrhizosphere microbial community are of special interest because some microorganisms associated with mycorrhiza may complement mycorrhizal activities (Toro et al. 1996). More recently, Frey-Klett et al. (2005) have proposed that the ectomycorrhizal symbiosis could be considered as a microbial complex where the fungal symbiosis has a direct effect on plant growth (nutritional and hormonal mechanisms) but also an indirect positive effect via a selective pressure on bacterial communities resulting, for instance, to a higher abundance of phosphate-solubilizing fluorescent pseudomonads in the hyphosphere. It has been previously demonstrated that P-solubilizing bacteria can interact synergistically with mycorrhizal fungi and improve the phosphorus nutrition of the host plant (Muthukumar et al. 2001).

To date, there is little information on the mechanisms controlling interactions between mycorrhizal fungi, soil bacteria and plant roots in the mycorrhizosphere. Although these interactions can influence the fungal symbiont itself and the plant and soil nutrient cycling processes, knowledge of these impacts and their

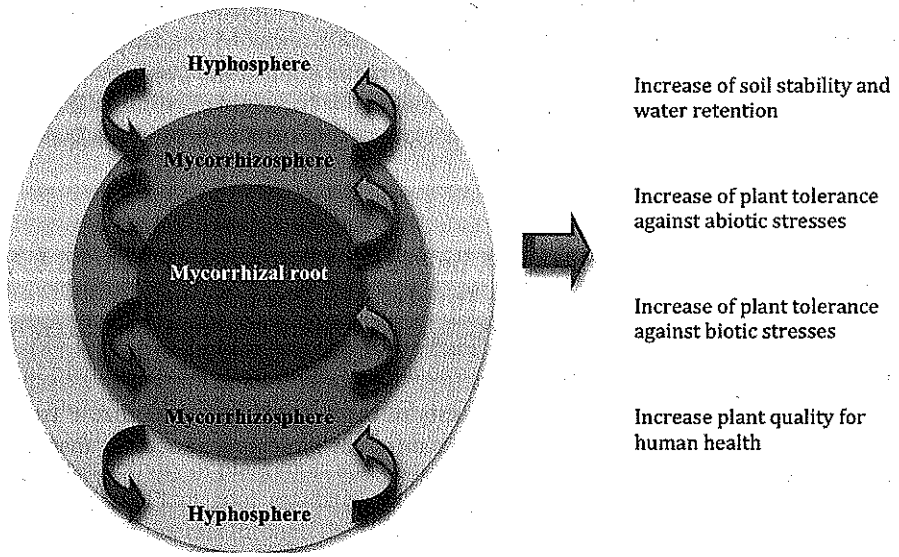

Fig. 5.1 The Mycorrhizosphere trophic complex and its role as an ecosystem service provider

consequences on soil biofunctioning and ecosystem productivity remains poorly understood (Fig. 5.1). On one hand, some soil bacteria can act as mycorrhization helper bacteria (MHB) by improving the establishment of the mycorrhizal symbiosis and on the other hand, mycorrhizal fungi can have an impact on the structure and functional diversity of bacterial communities (Assigbetse et al. 2005; Artursson et al. 2005). The purpose of this chapter is to outline the mycorrhizosphere interactions between ectomycorrhizal fungi associated with forest tree species and soil microflora of potentially synergistic properties that lead to stimulation of plant growth. By focussing on the ectomycorrhizal symbiosis associated with Tropical and Mediterranean tree species, we will review the global effects of ectomycorrhizal symbiosis on the functional diversity of soil microflora and in particular, the interactions between ectomycorrhizal fungi and some plant-growth-promoting rhizobacteria (i.e. rhizobia, fluorescent pseudomonads). It is well known that ectomycorrhizal fungi improve the phosphorus uptake of their associated host plant and enhance the plant development (Read and Perez-Moreno 2003). This ectomycorrhizal effect on plant growth has been mainly ascribed to the fact that the extramatrical mycelium increased the abilities of the host plant to explore a larger volume of soil than roots alone and to uptake nutrients from a greater surface area through different biological processes (Smith and Read 2008). Phosphorus (P) is one of the most essential macronutrients required for the growth and development of plant (Illmer and Schinner 1992) and occurs in various organic and inorganic forms not directly assimilable by plants and soil microorganisms. In degraded areas, the first objective of the controlled mycorrhization processes is to improve reforestation in areas presenting a loss or

reduction of major physico-chemical and biological soil properties (Requena et al. 2001) and more particularly severe phosphorus deficiencies. This review aimed to state the interactions between ectomycorrhizal fungi and soil microflora leading to a sustainable microbial complex with high efficiency against phosphorus mobilization and transferring phosphorus from the soil organic matter (SOM) or from soil minerals to the host plant.

5.2 Soil Microbial Processes Involved in Phosphorus Mobilization from Soil Organic Matter and Soil Minerals

Ectomycorrhizal fungi enhance the capacity of the host plants to mobilize P from soil inorganic and organic forms through different biological processes that are summarized below.

5.2.1 Mobilization of P from Soil Organic Matter

Soil organic matter contains a wide range of complex molecules such as inositol phosphate, nucleotides and phospholipids (Criquet et al. 2004). Soil microbes can degrade P-compounds through their capacity to produce a wide range of extracellular and surface-bound enzymes leading to the release into the soil of smaller organic compounds that provide potential sources of P for plants, ectomycorrhizal fungi and other soil microorganisms (Nahas et al. 1982; Haas et al. 1992). Phosphatase activities (acid and alkaline phosphatase) release orthophosphate ions (Pi) that are the unique form of P easily assimilable by soil microorganisms and plants (Rao et al. 1996). Enzymes can be free in the soil solution or bound to soil colloids, to humic substances, to living and dead microbial cells or to plant roots. Acid phosphatase activity in the rhizosphere may also be due to plant roots (Goldstein et al. 1988; Coello 2002), bacteria (Palacios et al. 2005; Boyce and Walsh 2007) and fungi (Yoshida et al. 1989; Weber and Pitt 1997; Bernard et al. 2002). The secretion of acid phosphatases is induced by Pi-deficient conditions for all the organisms studied (Goldstein et al. 1988; Bernard et al. 2002). Most of the studies performed in laboratory conditions with known substrates showed that these enzymatic activities are generally not substrate specific, except for phytases (Wyss et al. 1999), and are able to release Pi from different phosphorylated substrates. Phosphatase activity has often been used as a general indicator in measurements of biological activity (Joner and Johansen 2000). Ectomycorrhizal fungi differ in their physiological capacities to acquire and transfer nutrients to a range of plant hosts (Abuzinadah and Read 1989; Dighton et al. 1993; Bending and Read 1995). It has been suggested that ectomycorrhizal fungi contribute to organic P mobilization

from soil solution through the production of extracellular acid phosphatase (Quiquampoix and Mousain 2005). This beneficial effect (enhancement P nutrition of the host plant) is generally attributed to the development of external hyphae into the soil resulting in higher of soil volume exploited compared with nonmycorrhizal roots (Louche et al. 2010).

5.2.2 Mobilization of P from Soil Minerals

Ectomycorrhizal fungi have the potential ability to mobilize and translocate essential plant nutrients from minerals (Landeweert et al. 2001). Weathering processes of minerals (transformation of rock-forming primary minerals into dissolved compounds and secondary mineral residues into the biological environment) result from the activity of plant roots and their associated microbiota (rhizosphere bacteria and fungi). Plant root exudates and root-associated microorganisms affect the stability of minerals through the production of organic acids, phenolic compounds, protons, siderophores and polysaccharides (Barker et al. 1997; Drever 1994; Drever and Vance 1994). Soluble organic acids affecting mineral weathering range from low to high molecular weight such as humic substances but low molecular weight (LMW) organic acids are considered to be the main agents of mineral dissolution because of their dual acidifying and complexing properties (Ochs 1996; Barker et al. 1998). Numerous studies have shown that ectomycorrhizal fungal strains could dissolve minerals by excreting organic acids. Among these organic acids excreted by ectomycorrhizal fungi, oxalate, citrate and malate are the strongest chelators of trivalent metals. Oxalic acid is known to have the highest acid strength (Gadd 1999). This organic acid is involved in the dissolution process of common soil minerals such as apatite, biotite, phlogopite and microline (Courty et al. 2010). Many ectomycorrhizal fungi excrete oxalic acid in pure culture (Paris et al. 1996), but this organic acid excretion is also observed with ectomycorrhizas (van Schöll et al. 2006) and hyphal mats (Wallander et al. 2003). However, most of these studies have been performed in pure cultures or in pot experiments and the real contribution of ectomycorrhizal fungi in mineral weathering remains difficult to determine in natural conditions (Landeweert et al. 2001; Courty et al. 2010).

5.3 Impact of the Controlled Ectomycorrhization on Soil Microbial Functions and Phosphorus Mobilization

In forest formations, extend of extraradical mycelium of ectomycorrhizas interconnect roots belonging to the same or different ECM tree species. This common mycorrhizal network (CMN) allows a transfer of C and nutrients between host

plants (Simard and Durall 2004). Hence, the ability of ectomycorrhizal fungi to mobilize phosphorus and to transfer Pi to the host plants through this common mycorrhizal network could be supplemented by their positive selective pressure on soil microbial functions (i.e. phosphatase activity). This CMN effect is of particular importance in Mediterranean and Tropical areas where it has been clearly demonstrated that land degradation is associated with reductions in the below ground microbial diversity and/or activity (Kennedy and Smith 1995; Garcia et al. 1997).

The functioning of soil microbial community is central to understand ecosystem-level processes such as decomposition and nutrient cycling. Various standardized methodologies have been developed to determine the microbial functional characteristics (i.e. enzymatic activities, Biolog™ method, etc.). Degens and Harris (1997) proposed a method that avoids the problem of the culturability of soil microbial populations under artificial conditions. This method is based on the measurement of the patterns of in situ catabolic potential (ISCP) of microbial communities by adding individual organic substrates directly to the soil and measuring the resulting respiration response. Patterns of ISCP provide a real time measure of microbial functional diversity and this kind of measurement has shown that microbial functional diversity responded to changed land use (Degens and Vojvodic-Vukovic 1999), cropping intensity (Sparling et al. 2000), soil organic status (Degens et al. 2000), successional sequences (Schipper et al. 2001) and stress or disturbance to the soil (Degens et al. 2001). The ISCP methodology has also been used to compare functional diversity among the different soil compatments influenced or not by ectomycorrhizal symbiosis (bulk soil, rhizosphere, mycorrhizosphere and hyphosphere). In the present review, differences between microbial functionalities of these soil compartments will be reported from controlled mycorrhization experiments performed in glasshouse and in field conditions with regards to the biological processes involved in P mobilization and plant nutrition.

5.3.1 *Patterns of ISCP Profiles of Microbial Communities Influenced by Ectomycorrhizal Symbiosis in Controlled Conditions*

A glasshouse experiment was performed with seedlings of *Uapaca bojeri*, an endemic Euphorbiaceae of Madagascar, planted in pots filled with a natural soil collected in a forest ecosystem. Other results have shown that this tree species was highly dependent to the ectomycorrhizal symbiosis that stimulated plant growth and P nutrition (Ramanankierana et al. 2007). The aim of this study was to characterize the functional diversity in each of the soil compartment influenced by ectomycorrhizal fungi. The results showed that the patterns of ISCP of microbial communities from each of the four compartments were very significantly different (Fig. 5.2). They also showed that microorganisms able to catabolize organic acids

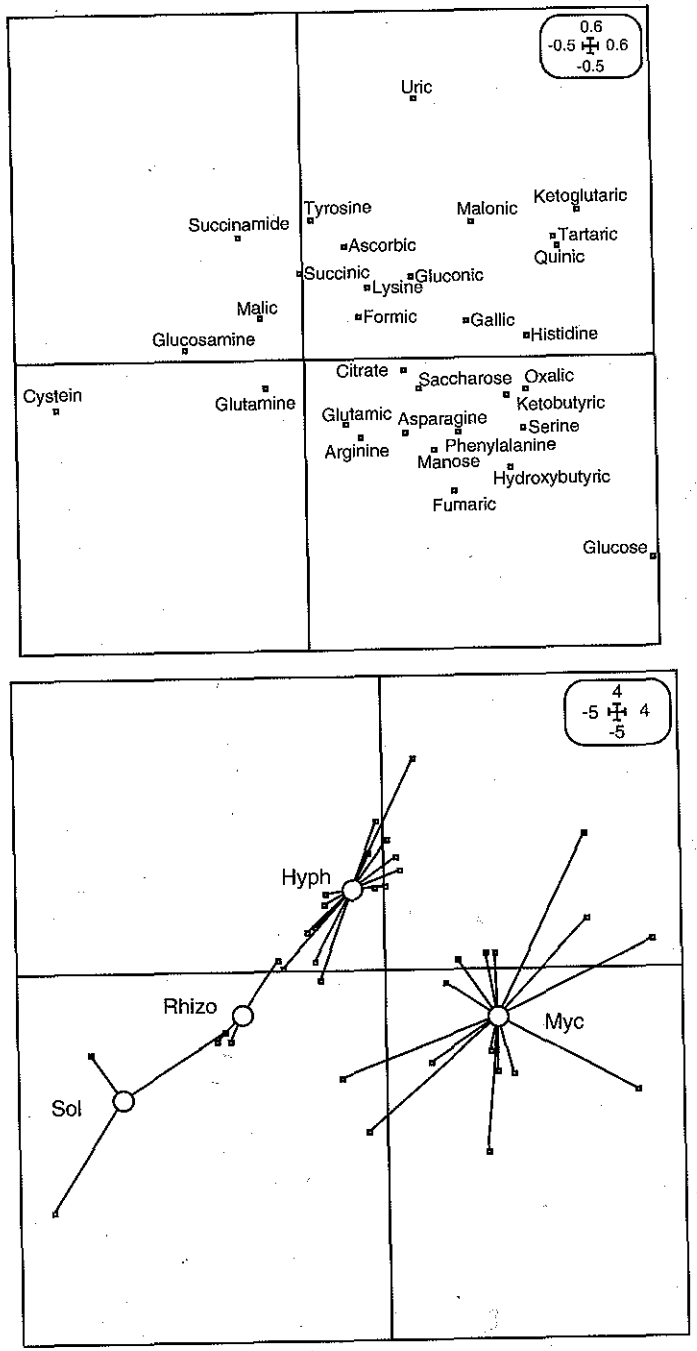

Fig. 5.2 Between-group analysis of the substrate induced respiration (SIR) responses of the bulk soil, rhizosphere, hyphosphere and mycorrhizosphere soil compartments. From Ramanankierana et al. (2006)

Table 5.1 Effect of ectomycorrhizal inoculation of *Pinus halepensis* with *Pisolithus* sp. on plant growth and needle nitrogen and phosphorus concentrations after 12-months culture in a non-disinfected soil (from Ouahmane et al. 2009)

	Treatments	
	Control (not inoculated)	*Pisolithus* sp.
Shoot biomass (mg dry weight)	312.2 (24.7) [(1)] a [(2)]	432.7 (21.5) b
Root biomass (mg dry weight)	159.7 (21.6) a	254.6 (21.8) b
Total biomass (mg dry weight)	480.9 (22.5) a	687.3 (21.6) b
Needle N content (%)	1.2 (0.1) a	1.5 (0.2) b
Needle P content (g kg^{-1})	4.1 (0.11) a	7.3 (0.13) b
Mycorrhizal colonization (%)	23.2 (1.5) a	52.5 (1.2) b

[(1)]Standard error of the mean. [(2)]Data in the same line followed by the same letter are not significantly different according to the Newman & Keuls test ($p < 0.05$)

were more abundant in the zone influenced by ectomycorrhizal fungi since it recorded a higher organic acid induced respiration in the mycorrhizosphere and hyphosphere. The authors conclude that ectomycorrhizal fungi through its exudates and more particularly through their organic acid productions induced a selective pressure on soil microbial communities. This kind of experiment has been replicated with *Pinus halepensis* and a strain of *Pisolithus* sp., selected for its high ability to mobilize P from inorganic form of phosphate (Ouahmane et al. 2009). The objective of this study was to assess how inoculation with an ectomycorrhizal fungus, *Pisolithus* sp., affects (1) the early growth of Aleppo pine seedlings and (2) the determination of functional diversity of soil microflora. After 12 months of culturing, ectomycorrhizal inoculation significantly improved the plant growth and nutrient uptake (N and P) (Table 5.1). *Pisolithus* inoculation induced strong modifications in soil microbial catabolic functions. In fact, Ectomycorrhizal inoculation led to higher average SIR responses with fumaric acid and citric acids (Fig. 5.3). This result suggested that large amounts of carboxylic acids excreted by the ectomycorrhizal fungus could exert a selective influence on soil microbial communities through a multiplication of carboxylic acids-, fumaric acid- and citric acid-catabolizing microorganisms inducing a higher SIR.

5.3.2 *Patterns of ISCP Profiles of Microbial Communities Influenced by Ectomycorrhizal Symbiosis in Field Conditions*

From our knowledge, the measurement of the patterns of in situ catabolic potential (ISCP) of microbial communities in a controlled mycorrhization experiment has been rarely realized with Mediterranean and Tropical tree species. Numerous studies have previously demonstrated that controlled mycorrhization could significantly improve the development of Australian acacias in glasshouse conditions (Cornet and Diem 1982; Duponnois et al. 2000; Duponnois and Plenchette 2003).

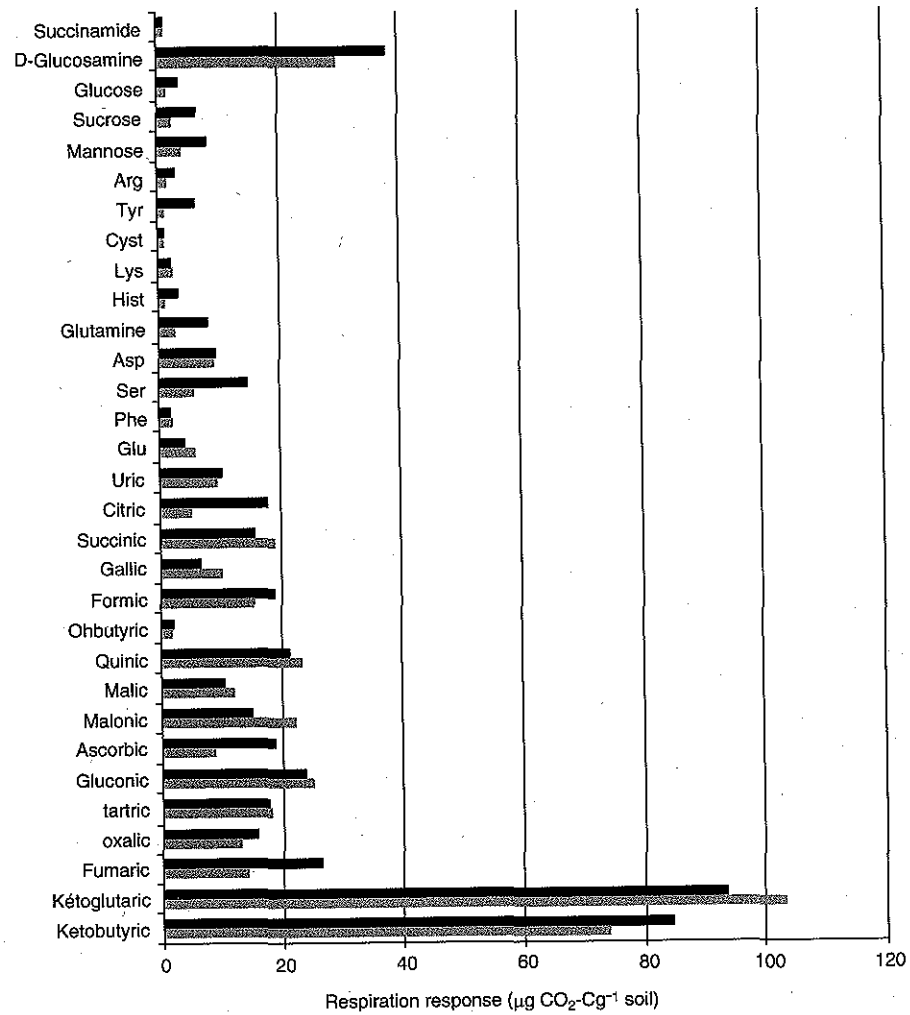

Fig. 5.3 Effect of ectomycorrhizal inoculation on soil catabolic responses. From Ouahmane et al. (2009)

However, data on the effect of mycorrhizal inoculation on host plant growth and biological soil properties in the field are very scarce. In Senegal, a field experiment was carried out to determine the effectiveness of the ectomycorrhizal inoculation with an isolate of *Pisolithus albus* (*P. albus* IR100) on the early development of an Australian *Acacia* species, *A. holosericea*, and on biological soil properties (Duponnois et al. 2005, 2007). After 2 years of plantation, ectomycorrhizal fungal inoculation significantly improved the diameter and the wood biomass of the *A. holosericea* trees as well as the N and P mineral contents per tree (Fig. 5.4).

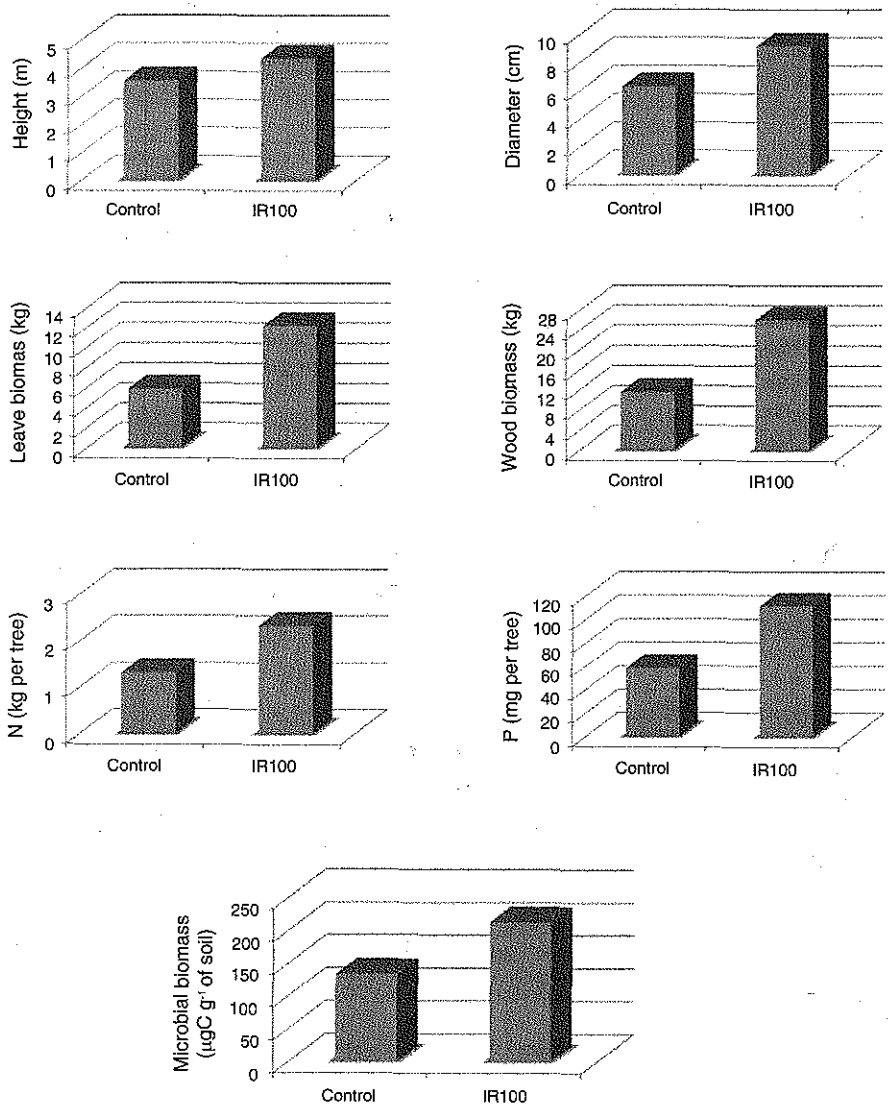

Fig. 5.4 Effect of fungal inoculation on tree growth, leaf mineral content and soil microbial biomass after 2 years of plantation in the field. From Duponnois et al. (2005)

Patterns of ISCP were determined in the soil collected out of the *A. holosericea* plantation (Crop soil), under uninoculated *A. holosericea* trees and under *Pisolithus* inoculated trees (Remigi et al. 2008). The results showed that ectomycorrhizal inoculation induced significant changes in the functions of soil microbial communities (Fig. 5.5).

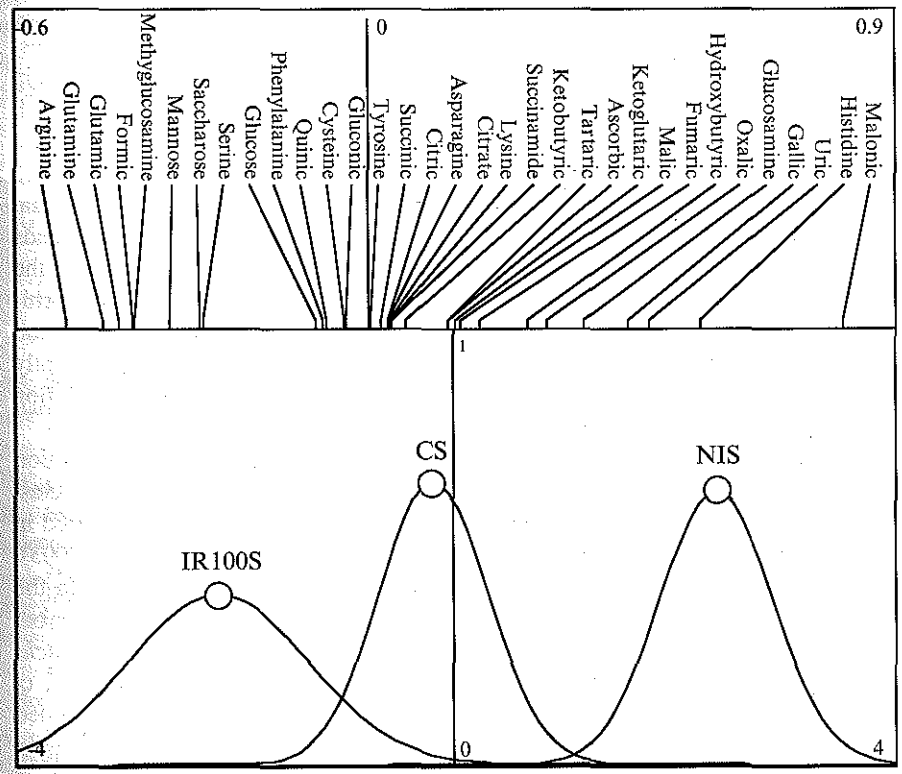

Fig. 5.5 Graphical display of the second BGA axis showing the SIRs with respect to the soil treatments. Only the second axis is used here, as the first axis merely separated the crop soil samples. The *upper part* of the figure shows the scores of the 33 substrates on the second BGA axis. In the *lower part*, the three Gauss curves represent the mean and variance of the scores of the nine soil samples (three repetitions for three treatments) on the second BGA axis. CS, crop soil; NIS, soil of plantation with uninoculated trees; IR100S, soil of plantation with *P. albus* IR100-inoculated trees. Substrates represented by *lines* curved in the same direction as corresponding Gauss curves tended to be used more in the corresponding soil samples. From Remigi et al. (2008)

5.4 Interactions Between Ectomycorrhizal Fungi and Selected PGPR

It has been already shown that some phosphate-solubilizing bacterial strains could interact with mycorrhizal fungi and enhanced plant P uptake (Kim et al. 1997; Toro et al. 1997; Muthukumar et al. 2001). These studies reported from the interactions between arbuscular mycorrhizal fungi and soil microflora. With regard to ectomycorrhizas, Frey-Klett et al. (2005) showed that phosphate-solubilizing bacteria were more abundant in the mycosphere of Douglas fir—*Laccaria bicolor* under symbiotic association and suggested that this enrichment could contribute to improve the nutrition of Douglas fir seedlings in the nursery soil. The positive

effect of the ectomycorrhizal symbiosis on this functional bacterial group was also recorded by Ramanankierana et al. (2006) who reported that the number of fluorescent pseudomonads was recorded in the mycosphere compartment similar to that in the mycorrhizosphere of hybrid larch, Sitka spruce and sycamore (Grayston et al. 1994), in the Douglas fir—*L. bicolor* mycorrhizosphere (Frey et al. 1997) and in the *A. holosericea—P. albus* mycorrhizosphere (Founoune et al. 2002a). In addition to this quantitative effect on fluorescent pseudomonads populations, ectomycorrhizal symbiosis has also modified the functional activities of fluorescent pseudomonads and, more particularly, in the mycosphere soil compartment. Thus, most of the P-solubilizing fluorescent pseudomonad strains were isolated from the mycorrhizosphere, suggested that the selective effect of the extramatrical mycelium can improve the bio-available phosphorus around the hyphae and, consequently enhanced the phosphorus uptake by the host plant directly from the soil solution or indirectly through the hyphal transfer.

The positive effect of the ectomycorrhizal symbiosis on the plant P nutrition could also stimulate the nodulation and N_2-fixation of leguminous tree species. Such effects of arbuscular mycorrhizal fungi on nodulation have been reported in *A. holosericea* with *Glomus intraradices* (Duponnois and Plenchette 2003), *G. fasciculatum* (Senghor 1998) and *G. mosseae* (Cornet and Diem 1982). In the same way, it has been shown that ectomycorrhizal fungi could enhance the number of rhizobial nodules per plant and increase nodule weight in Australian *Acacia* species namely *A. holosericea* and *A. mangium* (Founoune et al. 2002a, b, c; Duponnois et al. 2002; Duponnois and Plenchette 2003). These results suggested that the ectomycorrhizosphere effect induced chemical and physical changes in the soil around the roots but also in the physiological characteristics of the host plant that facilitate the development of rhizobia in the mycorrhizosphere soil compartment.

5.5 Conclusion

It is concluded that the ectomycorrhizal symbiosis can enhance plant growth through two trophic ways (1) directly on plant growth (hormonal and nutritional mechanisms) and (2) indirectly through a qualitative and quantitative effect on soil microflora. All these data showed the existence of soil multitrophic microbial associations resulting from interactions between the plants, the ecomycorrhizal fungal communities and soil microflora. Both biological processes underlined the major role of ectomycorrhizal symbiosis in soil functions and more particularly on soil biogeochemical cycles that ensure the nutrient availability for the cover plants. These fungal impacts on the genetic and functional diversity of soil microflora could have important implications for seedling establishment and, by extension, forest succession, dynamics and expansion. From a practical point of view, all these microbial factors have to be taken into account in improving the performance of afforestation programmes, especially in Mediterranean and Tropical areas.

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Cover illustration: Optical micrograph showing cross sections of intercellular colonization rice calli and regenerated plantlets by *A. caulinodans*: CS view of root uninoculated control; magnified cross section view of leaf colonized by *A. caulinodans* in regenerated rice plant; possible sites of infection and colonization of rice root (from left to right); see also Fig. 3.1 in "Endophytic Bacteria – Perspectives and Applications in Agricultural Crop Production", Senthilkumar M, R. Anandham, M. Madhaiyan, V. Venkateswaran, T.M. Sa, in "Bacteria in Agrobiology: Crop Ecosystems, Dinesh K. Maheshwari (Ed.)"

Background: Positive immunofluorescence micrograph showing reaction between cells of the rhizobial biofertilizer strain E11 and specific anti-E11 antiserum prepared for autecological biogeography studies; see also Fig. 10.6 in "Beneficial Endophytic Rhizobia as Biofertilizer Inoculants for Rice and the Spatial Ecology of this Bacteria-Plant Association", Youssef G. Yanni, Frank B. Dazzo, Mohamed I. Zidan in "Bacteria in Agrobiology: Crop Ecosystems, Dinesh K. Maheshwari (Ed.)"

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Preface

Bacteria are ubiquitous in nature: some of them are harmful but majority of them are beneficial to the plants. They comprise various attributes which directly and indirectly support plant growth and their fitness against adverse conditions of both abiotic and biotic in any given environmental system.

Coordinated interactions between microbes and plants are utmost important for their healthy association. Through this book we intend to provide a total of 18 chapters which signify the added advantages of bacteria, in general, and PGPR, in particular, in nutrient uptake and triggering defense responses of the plant against deleterious phytopathogens. Probiotics for plants exhibits multifarious functional characteristics beneficial in nature which lead to sustainable microbial complex ecosystem. Due to their diverse ecology, they exhibit multifarious functional characters beneficial in nature which lead to sustainable microbial complex ecosystem favorable to the host plants. Due to their probiotic nature and sometimes because of intimate association (example endophytes), they often serve as an alternative to fertilizers, herbicides, and chemical pesticides. A brief understanding of diversity, colonization, mechanism of action formulation, and application of such bacteria inoculants facilitate their contribution in the management of sustainable agroecosystem as exemplified by studying their responses on a plant model, *Arabidopsis*. Such bacteria have also been exploited in the improvement of quality of silk production. The probiotic nature of various group of bacteria found suitable candidates for combating fungal, bacterial nematode, and other diseases which are injurious to majority of plant besides conferring health benefits to above-ground plant parts and roots deep seated in soil. Some of the chapters highlight the impact of bacteria on soil structure and microbial community function that involved rhizosphere signals (molecules) apart from mediated systemic resistance for plants, potential for phosphorus nutrition application for microbial consortium, nitrogen fixation, and biofertilizer for eco-friendly low-input sustainable crop production. The book will benefit the teachers, researches students, and those interested in strengthening the subject of Agricultural Microbiology, Biotechnology, Plant Protection, Agronomy, and Environmental Sciences.

I wish to express my gratitude to all the subject experts who have provided their masterpiece work in giving the shape of the book. The work of several reviewers is