



## Mycorrhizosphere interactions to improve plant fitness and soil quality

José-Miguel Barea\*, Rosario Azcón & Concepción Azcón-Aguilar

Departamento de Microbiología del Suelo y Sistemas Simbióticos, Estación Experimental del Zaidín, CSIC, Prof. Albareda 1, 18008 Granada, Spain (\*Author for correspondence)

**Key words:** arbuscular mycorrhiza, biocontrol, N-fixing bacteria, PGPR, phosphate-solubilizing microorganisms, soil aggregation

### Abstract

Arbuscular mycorrhizal fungi are key components of soil microbiota and obviously interact with other microorganisms in the rhizosphere, i.e. the zone of influence of plant roots on microbial populations and other soil constituents. Mycorrhiza formation changes several aspects of plant physiology and some nutritional and physical properties of the rhizospheric soil. These effects modify the colonization patterns of the root or mycorrhizas (mycorrhizosphere) by soil microorganisms. The rhizosphere of mycorrhizal plants, in practice a mycorrhizosphere, harbors a great array of microbial activities responsible for several key ecosystem processes. This paper summarizes the main conceptual principles and accepted statements on the microbial interactions between mycorrhizal fungi and other members of rhizosphere microbiota and discusses current developments and future trends concerning the following topics: (i) effect of soil microorganisms on mycorrhiza formation; (ii) mycorrhizosphere establishment; (iii) interactions involved in nutrient cycling and plant growth; (iv) interactions involved in the biological control of plant pathogens; and (v) interactions to improve soil quality. The main conclusion is that microbial interactions in the rhizosphere of mycorrhizal plants improve plant fitness and soil quality, critical issues for a sustainable agricultural development and ecosystem functioning.

**Abbreviations:** PGPR – plant growth promoting rhizobacteria

### Introduction

The root-soil interfaces constitute a dynamic microcosm known as the *rhizosphere* where microorganisms, plant roots and soil constituents interact (Lynch 1990; Azcón-Aguilar & Barea 1992; Linderman 1992; Barea 1997, 2000, Kennedy 1998; Bowen & Rovira 1999). Carbon fluxes are critical for rhizosphere functioning (Toal et al. 2000). The rhizosphere is a physical, chemical and biological environment clearly distinct from the bulk soil, where altered microbial diversity and activity are characteristic (Kennedy & Smith 1995). The supply of photosynthates and decaying plant material to the root-associated microbiota, together with microbial-induced changes in rooting patterns, and the supply of available nutrients to plants, as derived from microbial activities, are key issues in rhizosphere formation and functioning. The release of organic material occurs mainly as root exudates, which act as either signals or growth

substrates (Werner 1998). Rhizosphere functioning is known to markedly influence plant fitness and soil quality because microbial developments in such environment can help the host plant to adapt to stress conditions concerning water and mineral deficit, and presence of soil-borne plant pathogens (Lynch 1990; Bethlenfalvay & Schüepp 1994; Bowen & Rovira 1999).

Mycorrhizal fungi are relevant members of the rhizosphere mutualistic microsymbiont populations known to carry out many critical ecosystem functions such as improvement of plant establishment, enhancement of plant nutrient uptake, plant protection against cultural and environmental stresses and improvement of soil structure (Smith & Read 1997). The fungi involved are microscopic in the case of the arbuscular mycorrhiza (hereafter *mycorrhiza*) formed by fungi in the order Glomales (Zigomycota) and more than 80% of the flowering plants (Barea et al. 1997). Mycorrhiza establishment is known to modify several aspects of

plant physiology including mineral nutrient composition, hormonal balance, C allocation patterns, etc. (Harley & Smith 1983; Smith et al. 1994; Azcón-Aguilar & Bago 1994). Consequently, the mycorrhizal symbiotic status changes the chemical composition of root exudates while the development of the fungal soil mycelium serves as a carbon source to rhizosphere microbial communities and introduces physical modifications into the environment surrounding the roots. These changes affect both quantitatively and qualitatively the microbial populations in the rhizosphere of the mycorrhizal plant also termed the *mycorrhizosphere* (Linderman 1992, 2000; Barea 1997, 2000; Cordier et al. 1999; Gryndler 2000). Though it could be conceptually accepted that the mycorrhizosphere is not strictly the rhizosphere of a mycorrhizal plant, it is difficult in practice to make any distinction (Bowen & Rovira 1999). In addition to mycorrhiza-induced changes in the rhizosphere there are specific modifications in the microenvironments surrounding the mycorrhizal mycelium itself, the *hyphosphere* (Gryndler 2000).

Two main groups of microorganisms interact with mycorrhizal fungi in the rhizosphere environments: saprophytes and symbionts. Both of them comprise detrimental, neutral and beneficial bacteria and fungi. Detrimental microbes include the major plant pathogens, as well as minor parasitic and non-parasitic, deleterious rhizosphere organisms (Weller & Thomashow 1994; Nehl et al. 1996). Beneficial microorganisms are known to play fundamental roles in soil-plant systems (Barea 1997). Particularly important is a subset of soil bacteria, namely the *rhizobacteria* (Kloepper 1994, 1996), known to display a specific ability for root colonization, with some of them able to improve plant development, therefore termed *plant growth promoting rhizobacteria* (PGPR). The PGPR carry out many important ecosystem processes, such as those involved in the biological control of plant pathogens, nutrient cycling and/or seedling establishment and soil quality (Kloepper et al. 1991; Lugtenberg et al. 1991; Haas et al. 1991; Lemanceau & Alabouvette 1993; O'Gara et al. 1994; Weller & Thomashow 1994; Glick 1995; Broek & Vanderleyden 1995; Bashan & Holguin 1998; Barea 2000; Jeffries & Barea 2001). Mycorrhizal fungi also interact with microorganisms colonizing root tissues, the endophytic microorganisms, which develop activities involved in plant growth promotion and plant protection (Kloepper 1994; Duijff et al. 1997; Van Loon et al. 1998; Sturz & Novak 2000). Mycorrhizal fungi also

interact with both symbiotic and free-living nitrogen ( $N_2$ )-fixing bacteria (Barea 1997).

Because of current public concerns about the side-effects of agrochemicals, more attention is now being given to research areas concerning biological balance in soil, microbial diversity or microbial dynamics in soil, etc. This is why the study of interactions in the mycorrhizosphere is a topic of current concern. Accordingly, the aim of this review is to summarize and discuss some key aspects including: (i) effect of soil microorganisms on mycorrhiza formation; (ii) mycorrhizosphere establishment (iii) interactions with symbiotic nitrogen-fixing bacteria, phosphate-solubilizing microorganisms, PGPR etc., which are involved in nutrient cycling and plant growth promotion; (iv) interactions for the biological control of root pathogens; and (v) interactions to improve soil quality concerning either soil aggregation, organic matter and nitrogen accumulation, or the decontamination of heavy metal polluted soils. These interactions will be described and discussed here from the point of view of their relevance in plant nutrition and health and in soil quality. The cellular and molecular aspects of these interactions are not in the aims of this study and have been recently discussed elsewhere (Bonfante & Perotto 2000; Franken & Requena 2001).

### Effect of soil microorganisms on mycorrhiza formation

Microbial populations in the rhizosphere are known to either interfere with or benefit mycorrhizal establishment (Germida & Walley 1996; Vosátka & Gryndler 1999). Deleterious rhizosphere bacteria (Nehl et al. 1996) and mycoparasitic relationships (Jeffries 1997), have been found to interfere with mycorrhiza formation, while many microorganisms can benefit mycorrhiza formation and/or functioning (Barea 1997). One example among the beneficial effects is that exerted by the so-called mycorrhiza helper bacteria known to stimulate mycelial growth of mycorrhizal fungi and/or enhance mycorrhizal formation (Garbaye 1994; Azcón-Aguilar & Barea 1995; Frey-Klett et al. 1997; Barea 1997; Gryndler & Hrselova 1998; Gryndler et al. 2000). Soil microorganisms can produce compounds that increase root cell permeability and are able to increase the rates of root exudation. This, in turn, would stimulate mycorrhizal fungal mycelia in the rhizosphere or facilitate root penetration by the fungus. Plant hormones, as produced by

soil microorganisms, are known to affect mycorrhiza establishment (Azcón-Aguilar & Barea 1992, 1995; Barea 1997, 2000).

Rhizosphere microorganisms are also known to affect the pre-symbiotic stages (Giovannetti 2000) of mycorrhizal development, like spore germination rate and mycelial growth (Azcón-Aguilar & Barea 1992, 1995). Several explanations have been proposed for the stimulatory effects of soil microorganisms on mycorrhizal fungal spores. These include: (i) detoxification of the medium, since microorganisms may remove inhibitors of fungal growth from the growth substrate; (ii) utilization of fungal self-inhibitors; (iii) production of stimulatory compounds such as water-soluble, diffusible substances or volatile products (or possibly both). Biologically active substances such as amino acids, plant hormones, vitamins and other organic compounds can be produced by soil microorganisms, and can stimulate the growth rates of mycorrhizal fungi. Volatile substances (CO<sub>2</sub>) could also be important (Azcón-Aguilar & Barea 1995). Detrimental effects of soil microorganisms on spore germination and mycelial growth in soil has also been reported (Linderman 1992, 1994; Azcón-Aguilar & Barea 1992, 1995).

It is noteworthy that antibiotic-producing *Pseudomonas* spp. (Barea et al. 1998; Vazquez et al. 2000) did not interfere with mycorrhiza formation or functioning.

### **Mycorrhizosphere establishment**

Mycorrhiza establishment changes both quantitatively and qualitatively the microbial populations in the rhizosphere (Azcón-Aguilar & Barea 1992; Linderman 1992; Barea 1997; Amora-Lazcano et al. 1998; Cordier et al. 1999). Large numbers of bacteria (including actinomycetes) and fungi are found associated with AM fungal structures (Filippi et al. 1998; Budi et al. 1999). Interestingly, some rhizobial and pseudomonad bacteria adhere to the hyphae of mycorrhizal fungi, which appear to be a vehicle for root colonization by these bacteria (Bianciotto et al. 2000). As Bianciotto et al. (2001) described, extracellular polysaccharides are involved in the attachment of *Azospirillum* and *Rhizobium* to mycorrhizal structures. An extreme case of close interactions is that of *Burkholderia* bacteria which have been identified as endosymbionts in mycorrhizal fungi of the Gigasporaceae (Bianciotto et al. 2000; Ruiz-Lozano & Bonfante 2000).

It is obvious that the mycorrhizosphere effect is due to the fact that the mycorrhizal mycelium releases energy-rich organic compounds responsible for an increased growth and activity of rhizosphere microorganisms in the hyphosphere. However, such a release of organic compounds is probably much lower than that produced by a mycorrhizal root, because bacteria counts in hyphospheric soil were lower than those in the rhizosphere as a whole (Andrade et al. 1997). Apparently, there is a preferential establishment of Gram-negative bacteria in the hyphosphere (Vosátka 1996).

It has been demonstrated that mycorrhizal colonization changes some morphological parameters in developing root systems (Atkinson et al. 1994; Berta et al. 1995), with a greater root branching as the most commonly described effect. Undoubtedly, these changes must affect establishment and activity of microorganisms in the mycorrhizosphere environment.

The establishment of microbial inoculants in the rhizosphere is affected by mycorrhizal co-inoculation (Christensen & Jakobsen 1993; Puppi et al. 1994; Barea 1997; Andrade et al. 1998a; Ravnskov et al. 1999). In particular, mycorrhizal inoculation improved the establishment of both inoculated and indigenous phosphate-solubilizing rhizobacteria (Toro et al. 1997; Barea et al. 2001).

### **Interactions involved in nutrient cycling**

The well-known activities of nitrogen-fixing bacteria and phosphate-solubilizing microorganisms improving the bioavailability of the major plant nutrients N and P, are very much enhanced in the rhizosphere of mycorrhizal plants where synergistic interactions of such microorganisms with mycorrhizal fungi have been demonstrated. Management of such interactions is a promising approach for either low-input agricultural technologies (Bethlenfalvai & Linderman 1992; Gianinazzi & Schüepp 1994; Jeffries & Barea 2001), or for the re-establishment of the natural vegetation in a degraded area (Miller & Jastrow 1994; Barea & Jeffries 1995).

A great deal of work has been carried out on the tripartite symbiosis legume (general term)-mycorrhiza-*Rhizobium* (general term) (Azcón-Aguilar & Barea 1992; Barea et al. 1992; Barea 2000). The inoculation of mycorrhizal fungi has been shown to improve nodulation and N<sub>2</sub> fixation. Because the use of the isotope <sup>15</sup>N has made it possible to ascertain and quantify

the amount of N which is actually fixed in a particular situation, the contribution of the mycorrhizal symbiosis to the process can be measured (Barea et al. 1992). The physiological and biochemical mechanisms underlying the mycorrhizal fungi  $\times$  *Rhizobium* interactions to improve legume productivity have been also discussed. In spite of the main mycorrhizal effect in enhancing *Rhizobium* activity is mediated by a generalized stimulation of host nutrition, more localized effects may occur at the root or nodule level (Barea et al. 1992). Interactions can also take place at either the pre-colonization stages, when both microorganisms interact as rhizosphere inhabitants, or during the development of the tripartite symbiosis (Azcón-Aguilar & Barea 1992). The influence of host and/or bacterial genotypes in these interactions has also been discussed, suggesting a certain specificity (Azcón et al. 1991; Ruíz-Lozano & Azcón 1993; Monzón & Azcón 1996).

The effects on mycorrhiza formation and function of a wild type (WT) *Rhizobium meliloti* strain were compared with those of its genetically modified (GM) derivative. This GM *Rhizobium* was developed to improve the nodulation competitiveness of the WT strain (Sanjuan & Olivares 1991). It was found that the GM rhizobial strain did not interfere with any process related to mycorrhiza formation by the mycorrhizal fungus *G. mosseae*, i.e. spore germination, mycelial growth from the mycorrhizal propagules and 'entry point' formation on the developing root system of the host plant *Medicago sativa*. Indeed, the GM *Rhizobium* increased the number of mycorrhizal colonization units and the nutrient acquisition ability in mycorrhizal plants, when compared with the WT rhizobial strain (Tobar et al. 1996). The establishment of the symbiotic interactions also induced changes in root morphology, in particular, the degree of branching increased and the number of lateral roots was higher in mycorrhizal plants inoculated with the GM *Rhizobium* strain (Barea et al. 1996). Measurements of the  $^{15}\text{N}/^{14}\text{N}$  ratio in plant shoots indicate an enhancement of the  $\text{N}_2$  fixation rates in *Rhizobium*-inoculated mycorrhizal plants with respect to those achieved by the same *Rhizobium* strain in non-mycorrhizal plants (Toro et al. 1998).

Multimicrobial interactions including not only mycorrhizal fungi and *Rhizobium* spp. but also PGPR have also been tested (Requena et al. 1997). These microorganisms were isolated from a representative area of a desertification-threatened semi-arid ecosystem in the south-east of Spain. Microbial isolates were char-

acterized and screened for effectiveness in soil microcosms. *Anthyllis cytisoides* L, a mycorrhiza-dependent pioneer legume, dominant in the target mediterranean ecosystem, was the test plant. Several microbial cultures from existing collections were also included in the screening process. In general, the results support the importance of physiological and genetic adaptation of microbes to the environment, thus the use of efficient local isolates is recommended. Several microbial combinations were effective in improving either plant development, nutrient uptake,  $\text{N}_2$ -fixation ( $^{15}\text{N}$ ) or root system quality showing that selective and specific functional compatibility relationships among the microbial inoculants were evident with respect to plant response.

Several experiments have demonstrated a positive effect of the interactions between mycorrhizal fungi and nodulating rhizobial bacteria under drought conditions (Goicoechea et al. 1997, 1998; Ruíz-Lozano et al. 2001).

*Rhizobium* strains have also been described to colonize the rhizosphere of non-legume hosts where they establish positive interactions with mycorrhizal fungi (Galleguillos et al. 2000).

The nitrogen-fixing *Azospirillum* bacteria are known to benefit plant development and yield under appropriate conditions (Okon 1994; Bashan 1999) and the main conclusions are that these bacteria mainly act by influencing the morphology, geometry and physiology of the root system. Interactions between mycorrhizal fungi and *Azospirillum* have been reviewed by Volpin & Kapulnik (1994) and it has been demonstrated that *Azospirillum* could enhance mycorrhizal formation and response while mycorrhizal fungi may improve *Azospirillum* establishment in the rhizosphere.

The interactions related to P-cycling have also received much attention. These are based on that the phosphate ions solubilized by free-living microorganisms from sparingly soluble inorganic and organic P compounds (Whitelaw 2000) increase the soil phosphate pools available for the extraradical arbuscular mycorrhizal mycelium to benefit plant nutrition (Smith & Read 1997). Several experiments have demonstrated synergistic microbial interactions involving phosphate solubilizing rhizobacteria (PSB) and mycorrhizal fungi (Barea et al. 1997; Kim et al. 1998). The interactive effect of PSB and mycorrhizal fungi on plant use of soil P sources of low bioavailability was evaluated by using  $^{32}\text{P}$  isotopic dilution approaches (Toro et al. 1997). The PSB behaved as

mycorrhiza-helper-bacteria, promoting mycorrhiza establishment by both the indigenous and the inoculated mycorrhizal fungi. Conversely, mycorrhiza formation increased the size of the PSB population. Because the bacteria did not change root weight, length or specific root length, they probably acted by improving the pre-colonization stages of mycorrhiza formation. The dual inoculation treatment significantly increased biomass and N and P accumulation in plant tissues and these dually inoculated plants displayed lower specific activity ( $^{32}\text{P}/^{31}\text{P}$ ) than their comparable controls, suggesting that the mycorrhizal and bacterized plants were using P sources (endogenous or added as rock phosphate) otherwise unavailable to the plant. It therefore appears that these rhizosphere/mycorrhizosphere interactions contributed to the biogeochemical P cycling, thereby promoting plant nutrition.

The interactive effect of phosphate-solubilizing bacteria, mycorrhizal fungi and *Rhizobium* with regard to improve the agronomic efficiency of rock phosphate for legume crops (*Medicago sativa*), was evaluated by using isotopic techniques under controlled conditions, and further validated under field conditions (Barea et al. 2002). It was demonstrated that the microbial interactions tested improved plant growth and N and P acquisition under normal cultivation. Similar results were obtained by using *Medicago arborea*, a woody legume of interest for revegetation and biological reactivation of desertified semi-arid Mediterranean ecosystems (Valdenegro et al. 2001).

### Interactions involved in the biological control of root pathogens

Mycorrhizal establishment has been shown to reduce damage caused by soil-borne plant pathogens (Azcón-Aguilar & Barea 1996; Cordier et al. 1999). Several mechanisms have been suggested to explain the enhancement of plant resistance/tolerance in mycorrhizal plants (Linderman 1994, 2000; Azcón-Aguilar & Barea 1996). One of the proposed mechanisms is based on the microbial changes produced in the mycorrhizosphere. In fact, there is strong evidence that these microbial shifts occur, and that the resulting microbial equilibria could influence the growth and health of the plants. Although this effect has not been specifically evaluated as a mechanism for mycorrhiza-associated biological control, there are indications that such a mechanism can be involved (Azcón-Aguilar & Barea 1992, 1996; Linderman 1994, 2000).

Early work showed that changes in the populations of soil microorganisms induced by mycorrhiza formation may lead to the stimulation of certain components of the resident microbiota that can be antagonistic to root pathogens. In this context, Meyer & Linderman (1986) found a lower number of sporangia and zoospores formed by cultures of *Phytophthora cinnamomi* by adding extracts of rhizosphere soil from mycorrhizal plants, and Secilia & Bagyaraj (1987) found that there were more pathogen-antagonistic actinomycetes in the rhizosphere of mycorrhizal plants than in that of non-mycorrhizal controls. Further studies have corroborated these findings and demonstrated that such an effect is dependent on the mycorrhizal fungus involved, as well as the substrate and host plant (Azcón-Aguilar & Barea 1996; Linderman 2000).

Rhizosphere microorganisms antagonistic to root pathogens are being used as biological control agents (Alabouvette et al. 1997). Therefore, there is a tendency to exploit the prophylactic ability of mycorrhizal fungi in association with these antagonists (Linderman 1994, 2000; Nemeč 1997; Barea et al. 1998; Budi et al. 1999). It should be noted that several studies have demonstrated that microbial antagonists of fungal pathogens, either fungi or PGPR, exert no antimicrobial effect against mycorrhizal fungi (Calvet et al. 1993; Barea, et al. 1998; Edwards et al. 1998; Vazquez et al. 2000).

### Interactions to improve soil quality

There is an increasing interest in applying mycorrhizal fungi in interaction with rhizobial strains to help revegetation of desertified ecosystems based on the use of shrub legumes belonging to the natural succession (Herrera et al. 1993; Requena et al. 2001). A number of experiments have aimed at assessing the long-term benefits of inoculation with these two types of plant microsymbionts not only on the establishment of target legume species, but also on the benefit induced by the symbiotically tailored seedlings in key physical-chemical soil properties (Requena et al. 2001). In fact, as a result of the degradation/desertification processes, disturbance of natural plant communities is often accompanied or preceded by the deterioration of physical-chemical and biological soil properties, such as structure, nutrient availability, organic matter content, microbial activity, etc. Therefore, it is becoming critical to recover these soil quality attributes by managing the mycorrhizosphere interactions (Barea &

Jeffries 1995; Schreiner et al. 1997; Miller & Jastrow 2000; Jeffries & Barea 2001).

A representative area within a desertified semi-arid ecosystem in southeast Spain was chosen for field studies on this topic. The existing natural vegetation was a degraded shrubland where *Anthyllis cytisoides*, a drought-tolerant legume able to form symbioses with both rhizobial bacteria and mycorrhizal fungi, was the dominant species (Requena et al. 1997). The interaction of these microsymbionts on seedling survival rates, growth, N-fixation, and N-transfer from N-fixing to non-fixing species associated in the natural succession, was studied together with the possible improvements of soil quality in terms of N content, organic matter levels, and the formation/stabilization of hydrostable soil aggregates in the rhizosphere of the target plants. A long-term improvement in the physico-chemical properties was evident in the soil around the *Anthyllis* plants inoculated with a mycorrhizal fungal inoculum based on indigenous taxa. The benefits included an increased N content, and a higher amount of organic matter and soil aggregation in the soil around the roots. It can be assumed that the increase in N content in the rhizosphere of the legume can be accounted for by an improvement in nodulation and N-fixation rates resulting from inoculation of nodulated plants with mycorrhizal fungi (Barea et al. 1992). The improvement of soil aggregation contributes to the maintenance of good water infiltration rates, good tilth and adequate aeration for plant growth, thus improving soil quality (Wright & Upadhyaya 1998). The important role of the extraradical mycelium in the formation of water-stable soil aggregates is well documented (Andrade et al. 1995, 1998b; Bethlenfalvai et al. 1999; Miller & Jastrow 2000), and the involvement of glomalin, a glycoprotein produced by the external hyphae of mycorrhizal fungi, has been demonstrated (Wright & Upadhyaya 1998). Glomalin has been suggested to contribute to hydrophobicity of soil particles and also, because of its glue-like hydrophobic nature, to participate in the initiation of soil aggregates.

Inoculation with native mycorrhizal fungi also benefited plant growth, N fixation and P acquisition by plants. Improved N status of non-leguminous plants grown in association with legumes has previously been described for agricultural crops (Azcón-Aguilar et al. 1979), but this was the first demonstration of this phenomenon for natural plant communities in a semi-arid ecosystem. The results support the general conclusion that the introduction of target indigenous plants species, associated with a managed community of

microbial symbionts, is a successful biotechnological tool to aid the recovery of desertified ecosystems. This can be envisaged as the initial steps in the restoration of a self-sustaining ecosystem.

Another aspects of mycorrhizosphere interactions with regard to improving soil quality concern applications to the phytoremediation of heavy metal polluted soils. This is an emergent field of mycorrhizal research. Studies by Azcón et al. (2001) demonstrated that the combined inoculation of mycorrhizal fungi and bacterial cultures, isolated from a contaminated environment was able to increase absorption of Zn and Cd from soil, and the subsequent translocation of the metals to plant shoot. This is a form of bioremediation (Wise et al. 2000). The environmental interest of cleaning contaminated areas supports further studies based in mycorrhizosphere interactions.

## Conclusions

From the reviewed information it can be stated that mycorrhizosphere interactions improve plant growth and health and soil quality, which are key issues for the sustainability of natural ecosystems as well as agroecosystems.

## Acknowledgments

This work was supported by CICYT-FEDER (1FD97-0763-CO3-02 project), Spain and the ECO-SAFE (QLRT-1999-31759 project) UE

## References

- Alabouvette C, Schippers B, Lemanceau P & Bakker PAHM (1997) Biological control of fusarium-wilts: towards development of commercial product. In: Boland GJ & Kuykendall LD (Eds) *Plant Microbe Interactions and Biological Control* (pp 15–36). Marcel Dekker, Inc., New York.
- Amora-Lazcano E, Vázquez MM & Azcón R (1998) Response of nitrogen-transforming microorganisms to arbuscular mycorrhizal fungi. *Biol. Fertil. Soil.* 27: 65–70.
- Andrade G, Azcón R & Bethlenfalvai GJ (1995) A rhizobacterium modifies plant and soil responses to the mycorrhizal fungus *Glomus mosseae*. *Appl. Soil Ecol.* 2: 195–202.
- Andrade G, Linderman RG & Bethlenfalvai GJ (1998a) Bacterial associations with the mycorrhizosphere and hyphosphere of the arbuscular mycorrhizal fungus *Glomus mosseae*. *Plant Soil* 202: 79–87.
- Andrade G, Mihara KL, Linderman RG & Bethlenfalvai GJ (1998b) Soil aggregation status and rhizobacteria in the mycorrhizosphere. *Plant Soil* 202: 89–96.

- Andrade G, Mihara KL, Linderman RG & Bethlenfalvay GJ (1997) Bacteria from rhizosphere and hyphosphere soils of different arbuscular mycorrhizal fungi. *Plant Soil* 192: 71–79.
- Atkinson S, Berta G & Hooker JE (1994) Impact of mycorrhizal colonisation on root architecture, root longevity and the formation of growth regulators. In: Gianinazzi S & Schüepp H (Eds) *Impact of Arbuscular Mycorrhizas on Sustainable Agriculture and Natural Ecosystems* (pp 47–60). ALS, Birkhäuser Verlag, Basel, Switzerland
- Azcón R, Vivas A, Ruíz-Lozano JM & Barea JM (2001) Effectiveness of indigenous arbuscular mycorrhizal (AM) fungi and bacterial isolates on plant growth and nutrition in Zn and Cd artificially contaminated soils. Book of abstracts, COST Action 838, Workshop on Managing arbuscular mycorrhizal fungi for improving soil quality and plant health in agriculture. June 7–9. University of Çukurova, Adana, Turkey. pp 50.
- Azcón R, Rubio R & Barea JM (1991) Selective interactions between different species of mycorrhizal fungi and *Rhizobium meliloti* strains, and their effects on growth, N<sub>2</sub>-fixation (<sup>15</sup>N) and nutrition of *Medicago sativa* L. *New Phytol.* 117: 399–404.
- Azcón-Aguilar C, Azcón R & Barea JM (1979) Endomycorrhizal fungi and *Rhizobium* as biological fertilizers for *Medicago sativa* in normal cultivation. *Nature* 27: 235–237.
- Azcón-Aguilar C & Bago B (1994) Physiological characteristics of the host plant promoting an undisturbed functioning of the mycorrhizal symbiosis. In: Gianinazzi S & Schüepp H (Eds) *Impact of Arbuscular Mycorrhizas on Sustainable Agriculture and Natural Ecosystems* (pp 47–60). ALS, Birkhäuser Verlag, Basel, Switzerland.
- Azcón-Aguilar C & Barea JM (1992) Interactions between mycorrhizal fungi and other rhizosphere microorganisms. In: Allen MJ (Ed) *Mycorrhizal Functioning. An Integrative Plant-fungal Process* (pp 163–198). Routledge, Chapman & Hall Inc., New York.
- Azcón-Aguilar C & Barea JM (1995) Saprophytic growth of arbuscular-mycorrhizal fungi. In: Hock B & Varma A (Eds) *Mycorrhiza Structure Function, Molecular Biology and Biotechnology* (pp 391–407). Springer-Verlag, Heidelberg.
- Azcón-Aguilar C & Barea JM (1996) Arbuscular mycorrhizas and biological control of soil-borne plant pathogens. An overview of the mechanisms involved. *Mycorrhiza* 6: 457–464.
- Barea JM (1997) Mycorrhiza/bacteria interactions on plant growth promotion. In: Ogoshi A, Kobayashi L, Homma Y, Kodama F, Kondon N & Akino S (Eds) *Plant Growth-promoting Rhizobacteria, Present Status and Future Prospects* (pp 150–158). OECD, Paris.
- Barea JM (2000) Rhizosphere and mycorrhiza of field crops. In: Toutant JP, Balazs E, Galante E, Lynch JM, Schepers JS, Werner D & Werry PA (Eds) *Biological Resource Management: Connecting Science and Policy* (OECD) (pp 110–125) INRA, Editions and Springer.
- Barea JM, Andrade G, Bianciotto V, Dowling D, Lohrke S, Bonfante P, O'Gara F & Azcón-Aguilar C (1998) Impact on arbuscular mycorrhiza formation of *Pseudomonas* strains used as inoculants for the biocontrol of soil-borne plant fungal pathogens. *Appl. Environ. Microbiol.* 64: 2304–2307.
- Barea JM, Azcón R & Azcón-Aguilar C (1992) Vesicular-arbuscular mycorrhizal fungi in nitrogen-fixing systems. In: Norris JR, Read DJ & Varma AK (Eds) *Methods in Microbiology* (pp 391–416). Academic Press, London.
- Barea JM, Azcón-Aguilar C & Azcón R (1997) Interactions between mycorrhizal fungi and rhizosphere microorganisms within the context of sustainable soil-plant systems. In: Gange AC & Brown VK (Eds) *Multitrophic Interactions in Terrestrial Systems* (pp 65–77). Blackwell Science, Oxford.
- Barea JM & Jeffries P (1995) Arbuscular mycorrhizas in sustainable soil plant systems. In: Hock B & Varma A (Eds) *Mycorrhiza Structure Function, Molecular Biology and Biotechnology* (pp 521–559). Springer-Verlag, Heidelberg.
- Barea JM, Tobar RM & Azcón-Aguilar C (1996) Effect of a genetically-modified *Rhizobium meliloti* inoculant on the development of arbuscular mycorrhizas, root morphology, nutrient uptake and biomass accumulation in *Medicago sativa* L. *New Phytol* 134: 361–369.
- Barea JM, Toro M, Orozco MO, Campos E & Azcón R (2002) The application of isotopic (<sup>32</sup>P and <sup>15</sup>N) dilution techniques to evaluate the interactive effect of phosphate-solubilizing rhizobacteria, mycorrhizal fungi and *Rhizobium* to improve the agronomic efficiency of rock phosphate for legume crops. *Nutr. Cycl. Agroecosyst* (in press).
- Bashan Y (1999) Interactions of *Azospirillum* spp. in soils: a review. *Biol. Fertil. Soils* 29: 246–256.
- Bashan Y & Holguin G (1998) Proposal for the division of plant growth-promoting rhizobacteria into two classifications: biocontrol-PGPB (plant growth-promoting bacteria) and PGPB. *Soil Biol. Biochem.* 30: 1225–1228.
- Berta G, Trotta A, Fusconi A, Hooker JE, Munro M, Atkinson D, Giovannetti M, Morini S, Fortuna P, Tisserant B, Gianinazzi-Pearson V & Gianinazzi S (1995) Arbuscular mycorrhizal induced changes to plant growth and root system morphology in *Prunus cerasifera*. *Tree Physiol.* 15: 281–293.
- Bethlenfalvay GJ, Cantrell IC, Mihara KL & Schreiner RP (1999) Relationships between soil aggregation and mycorrhizae as influenced by soil biota and nitrogen nutrition. *Biol. Fertil. Soils* 28: 356–363.
- Bethlenfalvay GJ & Linderman RG (1992) *Mycorrhizae in Sustainable Agriculture*. ASA Special publication No. 54, Madison, Wisconsin.
- Bethlenfalvay GJ & Schüepp H (1994) Arbuscular mycorrhizas and agrosystem stability. In: Gianinazzi S & Schüepp H (Eds) *Impact of Arbuscular Mycorrhizas on Sustainable Agriculture and Natural Ecosystems*. (pp 117–131). Birkhäuser, Basel.
- Bianciotto V, Andreotti S, Balestrini R, Bonfante P & Perotto S (2001) Mucoid mutants of the biocontrol strain *Pseudomonas fluorescens* CHA0 show increased ability in biofilm formation on mycorrhizal and nonmycorrhizal carrot roots. *Mol. Plant. Microbe Interac.* 14: 255–260.
- Bianciotto V, Lumini E, Lanfranco L, Minerdi D, Bonfante P & Perotto S (2000) Detection and identification of bacterial endosymbionts in arbuscular mycorrhizal fungi belonging to the family Gigasporaceae. *Appl. Environ. Microbiol.* 66: 4503–4509.
- Bonfante P & Perotto S (2000) Outside and inside the roots: Cell-to-cell interactions among arbuscular mycorrhizal fungi, bacteria and host plants. *Curr. Adv. Mycorrhizae Res.* 141–155.
- Bowen GD & Rovira AD (1999) The rhizosphere and its management to improve plant growth. *Adv. Agron.* 66: 1–102.
- Broek AV & Vanderleyden J (1995) Genetics of the *Azospirillum*-plant root association. *Crit. Rev. Plant Sci.* 14: 445–466.
- Budi SW, Van Tuinen D, Martinotti G & Gianinazzi S (1999) Isolation from *Sorghum bicolor* mycorrhizosphere of a bacterium compatible with arbuscular mycorrhiza development and antagonistic towards soilborne fungal pathogens. *Appl. Environ. Microbiol.* 65: 5148–5150.
- Calvet C, Pera J & Barea JM (1993) Growth response of marigold (*Tagetes erecta* L.) to inoculation with *Glomus mosseae*, *Trichoderma aureoviride* and *Phytophthora ultimum* in a peat-perlite mixture. *Plant Soil* 148: 1–6.

- Christensen H & Jakobsen I (1993) Reduction of bacterial growth by a vesicular-arbuscular mycorrhizal fungus in the rhizosphere of cucumber (*Cucumis sativus* L.). *Biol. Fertil. Soils* 15: 253–258.
- Cordier C, Lemoine MC, Lemanceau P, Gianinazzi-Pearson V & Gianinazzi S (1999) The beneficial rhizosphere: a necessary strategy for microplant production. *Acta Horticulturae* 530: 259–265.
- Duijff BJ, Gianinazzi-Pearson V & Lemanceau P (1997) Involvement of the outer membrane lipopolysaccharides in the endophytic root colonization of tomato roots by biocontrol *Pseudomonas fluorescens* strain WCS417r. *New Phytol.* 135: 325–334.
- Edwards SG, Young JPW & Fitter AH (1998) Interactions between *Pseudomonas fluorescens* biocontrol agents and *Glomus mosseae*, an arbuscular mycorrhizal fungus, within the rhizosphere. *FEMS Microbiol. Lett.* 116: 297–303.
- Filippi C, Bagnoli G, Citernesi AS & Giovannetti M (1998) Ultrastructural spatial distribution of bacteria associated with sporocarps of *Glomus mosseae*. *Symbiosis* 24: 1–12.
- Franken P & Requena, N (2001) Analysis of gene expression in arbuscular mycorrhizas: new approaches and challenges. *New Phytol.* 150: 517–523.
- Frey-Klett P, Garbaye J, Berge O & Heulin T (1997) Metabolic and genotypic fingerprinting of fluorescent Pseudomonads associated with the Douglas Fir-*Laccaria bicolor* mycorrhizosphere. *Appl. Environ. Microbiol.* 63: 1852–1860.
- Galleguillos C, Aguirre C, Barea JM & Azcón R (2000) Growth promoting effect of two *Sinorhizobium meliloti* strains (a wild type and its genetically modified derivative) on a non-legume plant species in specific interaction with two arbuscular mycorrhizal fungi. *Plant Sci.* 159: 57–63.
- Garbaye J (1994) Helper bacteria: A new dimension to the mycorrhizal symbiosis. *New Phytol.* 128: 197–210.
- Germida JJ & Walley FL (1996) Plant growth-promoting rhizobacteria alter rooting patterns and arbuscular mycorrhizal fungi colonization of field-grown spring wheat. *Biol. Fertil. Soils* 23: 113–120.
- Gianinazzi S & Schüepp H (1994) Impact of Arbuscular Mycorrhizas on Sustainable Agriculture and Natural Ecosystems. ALS, Birkhäuser Verlag, Basel.
- Glick BR (1994) Helper bacteria: The enhancement of plant growth by free-living bacteria. *Can. J. Microbiol.* 41: 109–117.
- Giovannetti M (2000) Spore germination and pre-symbiotic mycelial growth. In: Kapulnik Y & Douds DD Jr (Ed) *Arbuscular Mycorrhizas: Physiology and Function* (pp 3–18). Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Goicoechea N, Antolín MC & Sánchez-Díaz M (1997) Influence of arbuscular mycorrhizae and *Rhizobium* on nutrient content and water relations in drought stressed alfalfa. *Plant Soil* 192: 261–268.
- Goicoechea N, Szalai G, Antolín MC, Sánchez-Díaz M & Paldi E (1998) Influence of arbuscular mycorrhizae and *Rhizobium* on free polyamines and proline levels in water-stressed alfalfa. *J. Plant Physiol.* 153: 706–711.
- Gryndler M (2000) Interactions of arbuscular mycorrhizal fungi with other soil organisms. In: Kapulnik Y & Douds DD Jr (Ed) *Arbuscular Mycorrhizas: Physiology and Function* (pp 239–262). Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Gryndler M & Hrselova H (1998) Effect of diazotrophic bacteria isolated from a mycelium of arbuscular mycorrhizal fungi on colonization of maize roots by *Glomus fistulosum*. *Biol. Plant* 41: 617–621.
- Gryndler M, Hrselová H & Striteská D (2000) Effect of soil bacteria on growth of hyphae of the arbuscular mycorrhizal (AM) fungus *Glomus claroideum*. *Folia Microbiol.* 45: 545–551.
- Haas D, Keel C, Laville J, Maurhofer M, Oberliansli T, Schnider U, Voisard C, Wüthrich B & Defago G (1991) Secondary metabolites of *Pseudomonas fluorescens* strain CHA0 involved in the suppression of root diseases. In: Hennecke H & Verma DPS (Eds) *Advances in Molecular Genetics of Plant-microbe Interactions* (pp 450–456). Kluwer Academic Publisher, Dordrecht.
- Harley JL & Smith SE (1983) *Mycorrhizal Symbiosis*. Academic Press, New York.
- Herrera MA, Salamanca CP & Barea JM (1993) Inoculation of woody legumes with selected arbuscular mycorrhizal fungi and rhizobia to recover desertified mediterranean ecosystems. *Appl. Environ. Microbiol.* 59: 129–133.
- Jeffries P (1997) Mycoparasitism. In: Wicklow Söderström (Eds) *The Mycota IV Environmental and Microbial Relationships* (pp. 149–164). Springer-Verlag, Berlin, Heidelberg.
- Jeffries P & Barea JM (2001) Arbuscular Mycorrhiza – a key component of sustainable plant-soil ecosystems. In: Hock B (Ed) *The Mycota. Vol. IX Fungal Associations* (pp 95–113). Springer-Verlag, Berlin, Heidelberg.
- Kennedy AC (1998) The rhizosphere and spermosphere In: Sylvia DM, Fuhrmann JJ, Hartel PG & Zuberer DA (Eds) *Principles and Applications of Soil Microbiology* (pp 389–407). Prentice Hall, Upper Saddle River, New Jersey.
- Kennedy AC & Smith KL (1995) Soil microbial diversity and the sustainability of agricultural soils. *Plant Soil* 170: 75–86.
- Kim KY, Jordan D & McDonald GA (1998) Effect of phosphate-solubilizing bacteria and vesicular-arbuscular mycorrhizae on tomato growth and soil microbial activity. *Biol. Fertil. Soils* 26: 79–87.
- Klopper JW (1994) Plant growth-promoting rhizobacteria (other systems) In: Okon Y (Ed) *Azospirillum/plant associations* (pp 111–118). CRC Press, Boca Raton.
- Klopper JW (1996) Host specificity in microbe-microbe interactions. *BioScience* 46: 406–409.
- Klopper JW, Zablotowick RM, Tipping EM & Lifshitz R (1991) Plant growth promotion mediated by bacterial rhizosphere colonizers. In: Keister DL & Cregan PB (Eds) *The Rhizosphere and Plant Growth* (pp 315–326). Kluwer Academic Publishers, Dordrecht.
- Lemanceau P & Alabouvette C (1993) Suppression of Fusarium-wilts by fluorescent pseudomonads: mechanisms and applications. *Biocontrol Sci. Technol.* 3: 219–234.
- Linderman RG (1992) Vesicular-arbuscular mycorrhizae and soil microbial interactions. In: Bethlenfalvay GJ & Linderman RG (Eds) *Mycorrhizae in Sustainable Agriculture* (pp 45–70). ASA Spec. Publ., Madison, Wisconsin.
- Linderman RG (1994) Role of VAM fungi in biocontrol. In: Pflieger FL & Linderman RG (Eds) *Mycorrhizae and Plant Health* (pp 1–26). APS Press, St Paul.
- Linderman RG (2000) Effects of mycorrhizas on plant tolerance to diseases. In: Kapulnik Y & Douds DD Jr (Ed) *Arbuscular Mycorrhizas: Physiology and Function* (pp 345–365). Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Lugtenberg BJJ, Weger de LA & Bennett JW (1991) Microbial stimulation of plant growth and protection from disease. *Curr. Opin. Microbiol.* 2: 457–464.
- Lynch JM (1990) *The Rhizosphere*. John Wiley, New York.
- Meyer JR & Linderman RG (1986) Response of subtterranean clover to dual inoculation with vesicular arbuscular mycorrhizal fungi and a plant growth promoting bacterium, *Pseudomonas putida*. *Soil Biol. B* 18: 185–190.
- Miller RM & Jastrow JD (1994) Vesicular-arbuscular mycorrhizae and biogeochemical cycling. In: Pflieger FL & Linderman RG (Eds) *Mycorrhizae and Plant Health* (pp 189–212). APS Press, St. Paul, MN.

- Miller RM & Jastrow JD (2000) Mycorrhizal fungi influence soil structure. In: Kapulnik Y & Douds DD Jr (Eds) Arbuscular Mycorrhizas: Physiology and Function (pp 3–18). Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Monzón A & Azcón R (1996) Relevance of mycorrhizal fungal origin and host plant genotype to inducing growth and nutrient uptake in *Medicago* species. *Agric. Ecosyst. Environ.* 60: 9–15.
- Nehl DB, Allen SJ & Brown JF (1996) Deleterious rhizosphere bacteria: An integrating perspective. *Appl. Soil Ecol.* 5: 1–20.
- Nemec S (1997) Longevity of microbial biocontrol agents in a planting mix amended with *Glomus intraradices*. *Biocontrol Sci. Technol.* 7: 183–192.
- O’Gara F, Dowling DN & Boesten B (1994) *Molecular Ecology of Rhizosphere Microorganisms*. VCH, Weinheim, Germany.
- Okon Y (1994) *Azospirillum*/plant Associations. CRC Press, Boca Raton.
- Puppi G, Azcón R & Höflich G (1994) Management of positive interactions of arbuscular mycorrhizal fungi with essential groups of soil microorganisms. In: Gianinazzi S & Schüepp H (Eds) *Impact of Arbuscular Mycorrhizas on Sustainable Agriculture and Natural Ecosystems* (pp 201–215). ALS, Birkhäuser Verlag, Basel Switzerland.
- Ravnkov S, Nybroe O & Jakobsen I (1999) Influence of an arbuscular mycorrhizal fungus on *Pseudomonas fluorescens* DF57 in rhizosphere and hyphosphere soil. *New Phytol.* 142: 113–122.
- Requena N, Jimenez I, Toro M & Barea JM (1997) Interactions between plant-growth-promoting rhizobacteria (PGPR), arbuscular mycorrhizal fungi and *Rhizobium* spp. in the rhizosphere of *Anthyllis cytisoides*, a model legume for revegetation in mediterranean semi-arid ecosystems. *New Phytol.* 136: 667–677.
- Requena N, Perez-Solis E, Azcón-Aguilar C, Jeffries P & Barea JM (2001) Management of indigenous plant-microbe symbioses aids restoration of desertified ecosystems. *Appl. Environ. Microbiol.* 67: 495–498.
- Ruiz-Lozano JM & Bonfante P (2000) A *Burkholderia* strain living inside the arbuscular mycorrhizal fungus *Gigaspora margarita* possesses the *vacB* gene, which is involved in host cell colonization by bacteria. *Microbial Ecol.* 39: 137–144.
- Ruiz-Lozano JM & Azcón R (1993) Specificity and functional compatibility of VA mycorrhizal endophytes in association with *Bradyrhizobium* strains in *Cicer arietinum*. *Symbiosis* 15: 217–226.
- Ruiz-Lozano JM, Collados C, Barea JM & Azcón R (2001) Arbuscular mycorrhizal symbiosis can alleviate drought-induced nodule senescence in soybean plants. *New Phytol.* 151: 493–502.
- Sanjuan J & Olivares J (1991) Multicopy plasmids carrying the *Klebsiella pneumoniae* nifA gene enhance *Rhizobium meliloti* nodulation competitiveness on alfalfa. *Mol. Plant Micr. Interact.* 4: 365–369.
- Schreiner RP, Mihara KL, McDaniel H & Bethlenfalvai GJ (1997) Mycorrhizal fungi influence plant and soil functions and interactions. *Plant Soil* 188: 199–209.
- Secilia J & Bagyaraj DJ (1987) Bacteria and actinomycetes associated with pot cultures of vesicular arbuscular mycorrhizas. *Can. J. Micro.* 33: 1069–1073.
- Smith SE, Gianinazzi-Pearson V, Koide R & Cairney JWG (1994) Nutrient transport in mycorrhizas: structure, physiology and consequences for efficiency of the symbiosis. In: Robson AD, Abbott LK & Malajczuk N (Eds) *Management of Mycorrhizas in Agriculture, Horticulture and Forestry* (pp 103–113). Kluwer Academic Publishers, Dordrecht.
- Smith DE & Read DJ (1997) *Mycorrhizal Symbiosis*. Academic Press, London.
- Sturz AV & Nowak J (2000) Endophytic communities of rhizobacteria and the strategies required to create yield enhancing associations with crops. *Appl. Soil Ecol.* 15: 183–190.
- Toal ME, Yeomans C, Killham K & Meharg AA (2000) A review of rhizosphere carbon flow modelling. *Plant Soil* 222: 263–281.
- Tobar RM, Azcón-Aguilar C, Sanjuán J & Barea JM (1996) Impact of a genetically modified *Rhizobium* strain with improved nodulation competitiveness on the early stages of arbuscular mycorrhiza formation. *Appl. Soil Ecol.* 4: 15–21.
- Toro M, Azcón R & Barea JM (1997) Improvement of arbuscular mycorrhizal development by inoculation with phosphate-solubilizing rhizobacteria to improve rock phosphate bioavailability ( $^{32}\text{P}$ ) and nutrient cycling. *Appl. Environ. Microbiol.* 63: 4408–4412.
- Toro M, Azcón R & Barea JM (1998) The use of isotopic dilution techniques to evaluate the interactive effects of *Rhizobium* genotype, mycorrhizal fungi, phosphate-solubilizing rhizobacteria and rock phosphate on nitrogen and phosphorus acquisition by *Medicago sativa*. *New Phytol.* 138: 265–273.
- Valdenegro M, Barea JM & Azcón R (2001) Influence of arbuscular-mycorrhizal fungi, *Rhizobium meliloti* strains and PGPR inoculation on the growth of *Medicago arborea* used as model legume for re-vegetation and biological reactivation in a semi-arid mediterranean area. *Plant Growth Regulation* 34: 233–240.
- Van Loon LC, Bakker PAHM & Pieterse CMJ (1998) Systemic resistance induced by rhizosphere bacteria. *Annu. Rev. Phytopathol.* 36: 453–483.
- Vázquez MM, Cesar S, Azcón R & Barea JM (2000) Interactions between arbuscular mycorrhizal fungi and other microbial inoculants (*Azospirillum*, *Pseudomonas*, *Trichoderma*) and their effects on microbial population and enzyme activities in the rhizosphere of maize plants. *Appl. Soil Ecol.* 15: 261–272.
- Volpin H & Kapulnik Y (1994) Interaction of *Azospirillum* with beneficial soil microorganisms. In: Okon Y (Ed) *Azospirillum*/Plant Associations (pp 111–118). CRC Press, Boca Raton
- Vosátka M (1996) Soil bacteria – a component of plant, soil and arbuscular mycorrhizal fungal interactions. In: Azcon-Aguilar C & Barea JM (Eds) *Mycorrhizas in Integrated Systems – From Genes to Plant Development* (pp 613–618). European Commission Report EUR 16728, Brussels, Luxembourg.
- Vosátka M & Gryndler M (1999) Treatment with culture fractions from *Pseudomonas putida* modifies the development of *Glomus fistulosum* mycorrhiza and the response of potato and maize plants to inoculation. *Appl. Soil Ecol.* 11: 245–251.
- Weller DM & Thomashow LS (1994) Current challenges in introducing beneficial microorganisms into the rhizosphere. In: O’Gara F, Dowling DN, Boesten B & Weinheim VCH (Eds) *Molecular Ecology of Rhizosphere Microorganisms Biotechnology and the Release of GMOs* (pp 1–18). Germany .
- Werner D (1998) Organic signals between plants and microorganisms. In: Pinton R, Varanini Z & Nannipieri P (Eds) *The Rhizosphere: Biochemistry and Organic Substances at the Soil-Plant Interfaces*. Marcel Dekker Inc., New York.
- Whitelaw MA (2000) Growth promotion of plants inoculated with phosphate-solubilizing fungi. *Adv. Agron.* 69: 99–151.
- Wright SF & Upadhyaya A (1998) A survey of soils for aggregate stability and glomalin, a glycoprotein produced by hyphae of arbuscular mycorrhizal fungi. *Plant Soil* 198: 97–107.
- Wise DL, Trantolo DJ, Cichon EJ, Inyang HI & Stottmeister U (2000) *Bioremediation of Contaminated Soils*. Marcel Dekker, New York.