Mycorrhizal Interactions with the Rhizosphere Microflora: The Mycorrhizosphere Effect

R. G. Linderman

Supervisory research plant pathologist, Agricultural Research Service, United States Department of Agriculture, Horticultural Crops Research Laboratory, Corvallis, OR 97330.

Mycorrhizal fungi are ubiquitous in soils throughout the world and form symbiotic relationships with the roots of most terrestrial plants. Such relationships generally form in the presence of a myriad of microorganisms, and there is abundant literature to support the contention that some of those microbes interact in rather specific ways to influence the mycorrhizal relationship and its effects on plant growth. The purpose of this review is to describe the development of the mycorrhizosphere (i.e., the enhanced microbial activity in the soil around mycorrhizae as distinguished from that in the rhizosphere soil around nonmycorrhizal roots), to shed some light on the kinds of interactions that occur between mycorrhizal fungi and the soil microflora, and to underscore the need to evaluate plant responses to microbial inoculations in light of the mycorrhizosphere phenomenon. Discussions largely will be restricted to interactions with bacteria and fungi other than those involving nitrogen-fixing organisms and plant pathogens.

A wide diversity of fungal groups form several morphological types of mycorrhizal associations. For example, ectomycorrhizae are formed by many species of Basidiomycete and Ascomycete fungi, and only with members of the plant families Pinaceae, Betulaceae, Fagaceae, Salicaceae, and Myrtaceae. Some of the same fungi that form ectomycorrhizae may also form an ectendomycorrhizal relationship with members of the Ericaceae. Other ericaceous plants form an ericoid type of endomycorrhizal association with a restricted number of fungi, namely members of the general *Hymenoscyphus* (= *Pezizella*) (*Ascomycetes*), *Oidiodendron* (*Hyphomycetes*), and possibly *Clavaria* (*Basidiomycetes*). Orchids form a type of endomycorrhizal association with fungi in the form genus *Rhizoctonia* (*Deuteromycotina*). Most of the remainder of the plants on the earth form an endomycorrhizal type of association with members of the Endogonaceae, primarily in the genera *Glomus*, *Gigaspora*, *Sclerocystis*, *Acaulospora*, and *Entrophospora*. The latter relationship is typified by the production of vesicles and arbuscules within root cortical cells, and, thus, is referred to as vesicular-arbuscular or VA mycorrhizae.

Because the fungi and hosts of the various types of mycorrhizae are so different, it is important to recognize that aspects of the symbiosis may also be very different. Furthermore, the extent of our knowledge of details of these relationships varies greatly, a fact that will significantly affect any consideration of microbial interactions with mycorrhizae.

Major benefits from mycorrhizae. In the nearly ubiquitous symbiotic relationship between plant roots and mycorrhizal fungi, the latter have been shown to help plants acquire mineral nutrients from the soil, especially immobile elements such as P, Zn, and Cu, but also more mobile ions such as S, Ca, K, Fe, Mg, Mn, Cl, Br, and N (49). In soils where such elements may be deficient or otherwise less available, mycorrhizal fungi increase efficiency of mineral uptake, resulting in enhanced plant growth. Mycorrhizae also have been shown to increase water uptake and/or otherwise alter the plant's physiology to reduce stress response to soil drought (34,41). Furthermore, mycorrhizal fungi can reduce plant response to other soil stresses such as high salt levels; toxicities associated with mine spoils or land fills, heavy metals; or toxicities due to minor element imbalance such as Mn toxicity (49). Mycorrhizal fungi have in some cases reduced the disease response to plant pathogens due to some morphological or physiological change in the plant (14). Some mycorrhizal fungi produce metabolites that can alter the plant's ability to produce roots from cuttings or to alter root regeneration and root morphology,

resulting in greatly increased absorptive surface area and feeder root longevity (26,43). Mycorrhizal fungi are known also to alter soil texture by increasing the extent of soil particle aggregation and thus stability (47). A further benefit to some people is the production of edible mushrooms or truffles by certain ectomycorrhizal fungi while in their symbiotic associations.

Many of the mycorrhizal plant responses discussed above are the result of altered plant physiological processes. Increased uptake of mineral elements from soil will obviously alter the nutrient balance of the plant tissues. The carbon balance in plants will also change because of increased photosynthetic rate and altered carbon partitioning in mycorrhizal plants (35). The fact that mycorrhizal fungi have been shown to induce changes, usually increases, in phytohormone production (i.e., cytokinins, gibberellins, and ethylene) suggests that mycorrhizae play a key role by influencing regulatory systems in plants (1,7,17,43). One of the major changes in mycorrhizal plants is reduced membrane permeability (17), primarily due to increased P nutrition (38). Corresponding to the decreased membrane permeability is a change in the quality and quantity of root exudation (42) which, in turn, has the potential to induce a significant response in the rhizosphere microflora and microfauna.

Root morphology and function. Root morphology is commonly depicted as in Figure 1A, (similar to that of Rovira [40]), with root epidermal cells and root hair projections, cortex, stele, and a root cap somewhat surrounding a meristematic region. Roots offer structural support to the plant, function in the absorption of water and mineral nutrients, are the site of production of growth regulators such as cytokinins and gibberellins, are a site of starch storage, and provide a nutrient supply for a wide range of microorganisms (12,40). These nutrients are organic materials released into the rhizosphere as exudates (nonmetabolic leakage), secretions (metabolic release), plant mucilages, a mucigel, and lysates from sloughed cells. The root exudates and secretions are water soluble sugars, antibiotics, organic acids, and volatile compounds (19). The quality and quantity of these compounds can change significantly in response to a variety and combination of factors and conditions.

The rhizosphere effect. In 1904, Hiltner recognized the rhizosphere as that portion of the soil subject to the influence of plant roots and in which significant increased microbial activity occurs. Since then, many reviews (21,40) and even a recent book by Curl and Truelove (12) have discussed the concept and its implications to plant growth and health. All agree that the rhizosphere effect is a dynamic process initiated by root exudation and other release of organic nutrients and is influenced by host factors such as species, age, and stage of development; soil factors such as fertility, moisture level, and physical properties; environmental conditions such as light and temperature; cultural practices including foliage applications of chemicals; and soil microbial interactions. The rhizoplane and the surrounding rhizosphere soil are colonized or otherwise occupied by a wide range of microorganisms including saprophytes, a microfauna, innocuous endophytes, exopathogens, pathogens (parasitic), mycorrhizal fungi, and growth-promoting and deleterious rhizobacteria (12).

Development of mycorrhizae. Mycorrhizal fungi exist in soil as spores or as vegetative propagules in root fragments, not unlike other soilborne and most root-inhabiting fungi. Propagules of mycorrhizal fungi apparently respond to the stimulation of root exudates, and their hyphae or germ tubes grow and penetrate root epidermal cells. The colonization of host tissue progresses both internally and externally along the root surface, the latter resulting in initiation of new colonization sites. Depending on the host-symbiont combination, the colonization results in morphological and physiological changes in both host and fungus leading to the formation of an ecto-, ectendo-, ericoid, or endomycorrhizal relationship.

In the case of ectomycorrhizae, root morphology changes dramatically from the nonmycorrhizal state (compare Fig. 1A and C), i.e., loss of root hairs, the development of a thick fungal mantle surrounding the epidermis and cortex, and the development of extensive root branching. An extensive network of fungal hyphae and rhizomorphs forms that may extend some distance out into the surrounding soil. The increased root branching and hyphal network greatly increase the absorptive surface area.
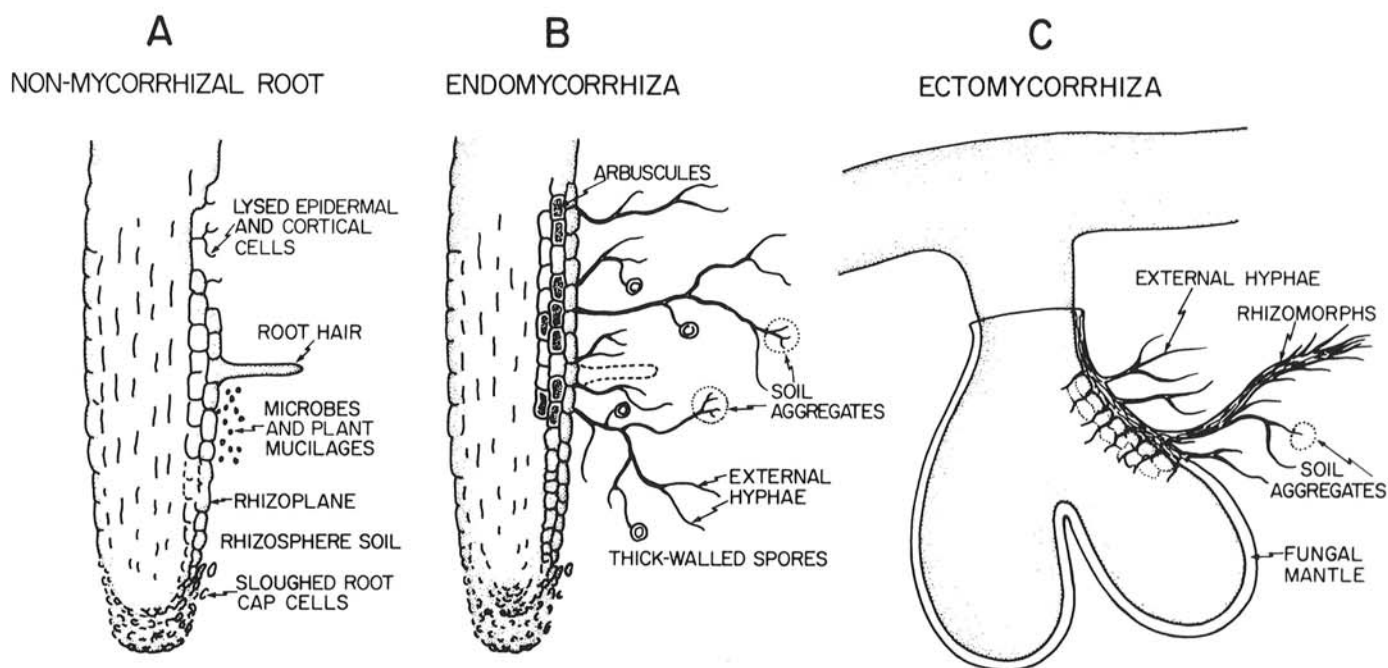

Fig. 1. Morphological changes in roots as they become mycorrhizal and the effects of those changes on the development of a mycorrhizosphere. **A,** Generalized nonmycorrhizal root (similar to that of Rovira [40]) with root hairs and indicated sources of organic materials available as substrates for rhizosphere microorganisms. **B,** Endomycorrhiza with indicated morphological changes such as reduced tissue sloughing, lack of root hairs; presence of external hyphae, thick-walled spores, and associated soil aggregates; and thickened endodermis (not shown); no obvious change in surface area. **C,** Ectomycorrhiza indicating dramatic morphological changes such as development of a fungal mantle plus extensive external hyphae and rhizomorphs and associated soil aggregates, loss of root hairs, and greatly increased branching and surface area.

With endomycorrhizae, development of the mycorrhizal state involves little obvious change in root morphology (compare Fig. 1A and B). In some plants, a yellow pigmentation accompanies root colonization, and the endodermis may become thickened. Generally, development of endomycorrhizae results in loss of root hairs, but no external fungal mantle forms except for the relatively sparse external hyphae that occur at the rhizoplane and extend out into the surrounding soil.

The physiological changes that accompany the development of mycorrhizae are undoubtedly extensive and by no means have they been completely characterized. The changes that would have the greatest impact on microorganisms in the surrounding soil, however, are the altered permeability of membranes, which will affect the quality and quantity of root exudation and secretions (38,42), and the changes in nutrient and elemental composition of the host tissues. These changes, coupled with the chemical and physical impact of the fungal symbiont hyphae in the surrounding soil, result in a very different potential in the rhizosphere, so different that Rambelli (37) suggested the term "mycorrhizosphere" be used to describe the soil surrounding and influenced by mycorrhizae.

The mycorrhizosphere effect. When mycorrhizae form, the symbiotic relationship significantly changes the physiology and/or morphology of roots and the plant in general. The changes in root exudates cause a new microbial equilibrium to be established. These changes presumably involve the same types of organisms as were involved in the rhizosphere before formation of mycorrhizae, but quantitative changes occur within these types as a result of direct metabolic interaction with the mycorrhizal fungus hyphae or spores, or the indirect effects mediated by the host. In most reports of microbial interactions in the mycorrhizosphere, no distinction between direct and indirect effects has been made.

The mycosphere effect. A key difference between the rhizosphere effect in soil around nonmycorrhizal roots and the mycorrhizosphere effect is the presence of mycorrhizal fungus extra-matrical hyphae that extend out some distance from the host tissues into the soil (18,39). The hyphae of VA mycorrhizae are relatively sparse compared with the profusion of hyphae and rhizomorphs that are associated with ectomycorrhizae. Regardless of type, however, extra-matrical hyphae of mycorrhizal fungi have a profound effect on the soil microflora, just as do fungal structures of other soilborne fungi. Gilbert and Linderman (16) suggested the term "mycosphere effect" to describe the enhanced microbial populations of selected microorganisms near fungal structures in soil. It has been shown that extra-matrical hyphae of VA mycorrhizal fungi exude substances that cause soil and organic fractions to aggregate (47). Microorganisms flourish in the aggregates, and fungi, bacteria, actinomycetes, and algae (including cyanobacteria) have been isolated from them (15). It has been shown with fungal root pathogens (16) that the microorganisms in the mycosphere are selectively favored by the fungal exudates, while others from the soil are not. The microbes in the mycosphere of mycorrhizal fungi may profoundly affect mycorrhizal functions, such as nutrient and water uptake, which are mediated by the extra-matrical hyphae. Because these hyphae or hyphal strands extend into the soil, they may also effectively extend the limits of the mycorrhizosphere considerably past the limits of the rhizosphere of nonmycorrhizal roots (39). Mycorrhizal extra-matrical hyphae are nutritionally supported by the host, but their biomass may be influenced by soil microorganisms and by soil factors such as pH, texture, fertility, and pesticide content (18,47).

Microbial interactions. The reported microbial interactions in the mycorrhizosphere may involve a variety of bacteria and fungi with specific functional capabilities that may influence plant growth. This may include microbes such as strict or facultative anaerobes, extracellular chitinase producers, phosphate solubilizers, siderophore producers, antibiotic producers, hormone producers, pathogen suppressors, plant growth promoters, exopathogens, mycorrhiza suppressors, etc. However, information is limited for many of these groups of organisms.

Orchid and ericoid mycorrhizae. I am not aware of any reports of microbial interaction with either orchid or ericoid mycorrhizae.

Ectomycorrhizae. Davey (13) reviewed the subject of microorganisms associated with developing and already-established mycorrhizae. Early studies showed an increased development of mycorrhizae if certain associative bacteria and fungi, such as *Azotobacter*, *Trichoderma*, and fluorescent pseudomonads, were also present at the time of inoculation. The mode of action proposed, but not documented, was the production of growth-promoting substances, such as thiamin, which stimulated both the plant roots and the mycorrhizal fungi. Davey (13) also reviewed reports suggesting that certain bacteria and fungi may also be detrimental to the development of mycorrhizae.

All the reports of microbial changes in the mycorrhizosphere of ectomycorrhizae have described a selective, qualitative change in the kinds of microbes found therein. At this date, no one has reported any dual inoculation studies or effects of ectomycorrhizae on specific functional groups of microbes that may influence plants in some manner. Katznelson et al (22) reported significant qualitative and quantitative differences in fungal, actinomycete, and bacterial populations in soil around mycorrhizal and nonmycorrhizal yellow birch. Oswald and Ferchau (33) reported that the bacteria isolated from coniferous roots without mycorrhizae were different from those that were mycorrhizal. Neal et al (31,32) reported differences in rhizosphere microbial populations between mycorrhizal and nonmycorrhizal Douglas-fir and red alder seedlings. Rambelli (37) reviewed the subject of microbial interactions in the mycorrhizosphere, including his own work on qualitative and quantitative changes. Most noteworthy of his own work was the description of the close association of nitrogen-fixing bacteria with the ectomycorrhizal mantle of *Pinus radiata*, wherein atmospheric nitrogen fixed by the bacteria was available for use by the fungus and plant host, and the bacteria could derive nutrients from the fungal hyphae. A similar association was reported more recently by Li and Castellano (24) for *Azospirillum* and fruiting bodies of ectomycorrhizal fungi associated with Douglas-fir. Bowen and Theodorou (10) isolated bacteria from the mycorrhizosphere soil around mycorrhizae of pine and demonstrated that some were deleterious and some beneficial to the in vitro growth of mycorrhizal fungi, but did not show that such microbes actually influenced the development of mycorrhizae or plant growth. Malajczuk and McComb (27) reported intriguing results comparing rhizosphere populations around mycorrhizal and nonmycorrhizal eucalyptus seedlings grown in soils suppressive or conducive to root rot caused by *Phytophthora cinnamomi* Rands. Their data showed that the microflora associated with mycorrhizae was distinctly different from that occurring on nonmycorrhizal roots, and high counts of bacteria were present throughout the mantle, both within and between symbiont cells. Furthermore, many bacteria were highly antagonistic to species of *Phytophthora* and *Pythium* causing root disease. In recent experiments, Schisler and Linderman (*unpublished*) have demonstrated that volatiles emanating from ectomycorrhizae exert a selective pressure on segments of the microflora, resulting in shifts in populations of bacteria. The dearth of information on microbial interactions in the mycorrhizosphere of ectomycorrhizae suggests it would be a fruitful area for future investigations, especially regarding specific microbes that may be used in dual inoculations with mycorrhizal fungi to give an additive or synergistic growth benefit to the host plant.

VA mycorrhizae. Microbial interactions in the mycorrhizosphere of VA mycorrhizae have been recently reviewed by Bagyaraj (5) and Barea and Azcon-Aguilar (8). As their reviews indicate, most of the reported interactions have focused on dual inoculations of selected bacteria and mycorrhizal fungi in relation to plant growth enhancement. Bagyaraj and Menge (6) reported an increase in rhizosphere populations of bacteria and actinomycetes when plants were inoculated with *Azotobacter* or VA mycorrhizae, inoculated singly or in combination, but more from the combination. Dual inoculation resulted in synergistic growth enhancement of the host plant. Meyer and Linderman (30) compared rhizoplane and rhizosphere soil in regard to the selection of qualitatively different functional groups of bacteria from the

naturally occurring microflora. They showed no quantitative difference in total bacteria in the rhizosphere soils from mycorrhizal and nonmycorrhizal plants, but significant qualitative shifts. For example, facultative anaerobes (possible nitrogen fixers and ethylene producers) increased in the mycorrhizosphere soil, but fluorescent pseudomonads decreased. Fluorescent pseudomonads significantly increased in the rhizoplane of mycorrhizal plants, however, as did the total number of bacteria. Their study also showed that microbial shifts had occurred in the mycorrhizosphere that adversely affected the microbe-influence on sporangial induction of the root pathogen *P. cinnamomi*. Ames et al (2) have also demonstrated that certain introduced bacteria were selectively influenced in rhizosphere soil by mycorrhizae. It seems apparent that some of these microbial shifts could influence or be directly involved in noted plant responses.

When selected bacteria have been used in dual inoculations with VA mycorrhizal fungi, significant interactions have resulted. For example, dual inoculations with VA mycorrhizal fungi and rhizobacteria have resulted in increased mycorrhizal colonization (6,29), possibly due to increased spore germination as demonstrated by Mayo et al (28). The majority of the other dual inoculation reports demonstrate that beneficial bacteria, such as symbiotic or free-living nitrogen fixers (6,9,46,48), phosphate solubilizers (3,36), or plant growth-promoting rhizobacteria (PGPR) (11,20,29), somehow work in tandem with mycorrhizal fungi to give additive or synergistic growth enhancement of the host plant. Meyer and Linderman (29) demonstrated that dual inoculation with VA mycorrhizal fungi and a growth-promoting pseudomonad induced an additive growth response on subclover (*Trifolium subterraneum* L.). Whether the two organisms interacted directly outside the host or indirectly via some physiological change in the host plant was not determined. Uptake of minor elements was increased by the dual inoculation, possibly because of increased colonization by the mycorrhizal fungi in the early stages of plant development. Also, increase in nodulation by *Rhizobium* was greatest when both VA mycorrhizal fungi and PGPR were used (29).

In cases of growth benefit by dual inoculation with mycorrhizal fungi and some rhizobacteria, it is assumed that each beneficial microbe contributes something toward enhanced plant growth, such as increased nitrogen or soluble phosphate. The mechanisms may be much more complex than that, however, and elucidating them should be the subject of future research. Furthermore, some of the bacteria involved may be interacting on more than one metabolic level, i.e., P solubilizers may also be auxin producers, or N fixers may also produce antibiotics (3,4,20,45).

Some bacteria may also have a suppressive effect on mycorrhiza formation and host response, such as that reported by Krishna et al (23) with *Streptomyces* and VA mycorrhizae. It is conceivable that frequent failures to successfully establish mycorrhizal fungi are due to microbial competition and suppressed colonization. Similarly, failure to demonstrate benefit from inoculation with some rhizobacteria may be due to the suppressive effect of competing bacteria.

Mycorrhizae and the general microflora. There have been some reports suggesting that the general microflora of the soil may have a significant influence on the formation of the mycorrhizal association. The development of extra-matrical hyphae of mycorrhizal fungi, for example, may be stimulated by the microflora. Sutton and Sheppard (47) showed that adding nonsterile soil leachate to a pasteurized soil increased the biomass of extra-matrical hyphae of VA mycorrhizae in some undetermined manner. St. John et al (44) showed that VA mycorrhiza formation was stimulated by a volatile compound, possibly ethylene (or some other compound easily oxidized by potassium permanganate), that could have been a product of the soil microflora. Bowen and Theodorou (10) showed that certain bacteria isolated from ectomycorrhizae could stimulate in vitro growth of the mycorrhizal fungi, but neither the mechanism of interaction nor the effect of the bacteria in vivo was studied. It seems reasonable to hypothesize that the soil microflora could stimulate the development of hyphal strands and rhizomorphs of

ectomycorrhizal fungi, but this too is a subject of future research.

Host responses to mycorrhizae reconsidered. Plants respond to the presence of mycorrhizae in a number of ways, as discussed earlier. It seems appropriate to reconsider those benefits attributed to mycorrhizae in light of the mycorrhizosphere interactions discussed here. The key question to ask is whether the host responses are due to the presence of mycorrhizae alone, to other beneficial rhizosphere microbes, or to their combination. For example, is increased P uptake by mycorrhizae a function of the increased absorption potential due to the development of extra-matrical hyphae, or is it due to the combined effect of those hyphae and hypha-associated P solubilizing bacteria? Are changes in root production and/or morphology due to products of the mycorrhizal fungus or associative bacteria? Is reduced root infection by pathogens due to effects of mycorrhizae and/or their products, or to effects of bacterial associates of the mycorrhizae and their products? Given the findings mentioned here, it seems reasonable to think that host responses to mycorrhizae are the net result of the mycorrhizal fungus plus its mycorrhizosphere associates. This question was also raised by Bagyaraj (5) in discussing the work by Williams (50) who observed that certain "companion fungi" occurred in high frequency in VA mycorrhizal pot cultures. Certain isolates of those companion fungi could stimulate, inhibit, or have no effect on plant growth. Where such fungi are present in VA mycorrhizal pot culture inoculum, are they or the mycorrhizal fungi responsible for growth enhancement when that inoculum is used? One count ask a similar question regarding the presence of certain bacterial associates that could occur in pot cultures or any nonsterile soil used in growth studies. In mycorrhiza experiments, careful control treatments are usually included to provide microbes that might influence growth responses independent of the mycorrhizal fungi. It may not be possible, however, to provide the same potential for such microorganisms to increase without the support of the mycorrhizal fungus itself in the treatment.

Host growth responses to rhizobacteria reconsidered. Beneficial rhizobacteria have been credited with having positive effects on the growth of plants (11). Growth enhancement effects from inoculation with these bacteria may be due to enhanced nutrient availability, production of growth regulating substances, or to pathogen suppression by antagonism or competition. In few instances where natural soil is used, however, has the involvement of mycorrhizal fungi been considered, even though they are known to be ubiquitous in terrestrial soil environments. Most plants (excluding aquatic plants and a few exceptional families) are rarely ever nonmycorrhizal unless the soil has been specifically treated with heat or chemicals, or roots are examined in the very early seedling stage before mycorrhizae have established. Because most of the groups of known beneficial rhizobacteria have been shown to positively interact with mycorrhizal fungi, it seems only likely that the benefits for which those bacteria are credited might also be the product of the interaction, at least where tests were conducted under natural soil conditions. In many cases, researchers should reevaluate their results in light of the probable impact of mycorrhizal fungi. Furthermore, many anomalies and inconsistencies that plague most studies in soil-related sciences might be explained if mycorrhizal fungi are considered as a possible uncontrolled variable in the experiments.

Managing the mycorrhizosphere. If our goal is to maximize beneficial plant growth responses, then optimum combinations of mycorrhizal fungi and selected bacteria should be used. This management strategy is well supported by the numerous reports already discussed wherein dual inoculations resulted in more growth enhancement than with either organism alone. It is important, therefore, to identify the best strains of beneficial microbes for the planting situation, verify their compatability and combined efficacy, and employ this combination inoculum in real agricultural situations as part of the management and production practices (25). Although this seems to be a very large task, it is possible if done systematically. Mycorrhizal fungi and bacterial associates must be characterized as completely as possible regarding the soil conditions they prefer, as well as the host plant

with which they were found associated. Tailoring the microbes to fit the growth situation will increase the chances of successful exploitation of the mycorrhizosphere phenomenon.

Conclusions. In light of these discussions based on considerable documentation in the literature, it seems reasonable to consider the following conclusions: 1) The mycorrhizosphere, as compared with the rhizosphere, is the rule, not the exception; 2) if we are to understand rhizosphere reactions and interactions, we must understand mycorrhizae and thus the mycorrhizosphere; 3) understanding the mycorrhizosphere will come from studying both internal host response as well as external interactions, including those in the mycosphere; and 4) there are significant experimental problems to overcome in studying the mycorrhizosphere, but the challenge is worth the effort and risk because the benefits could be tremendous. A better understanding of the mycorrhizosphere would allow effective management of microorganisms that could solve a number of unsolved plant growth and production problems.

LITERATURE CITED

1. Allen, M. F., Moore, T. S., Jr., and Christensen, M. 1980. Phytohormone changes in *Bouteloua gracilis* infected by vesicular-arbuscular mycorrhizae: I. Cytokinin increases in the host plant. Can. J. Bot. 58:371-374.
2. Ames, R. N., Reid, C. P. P., and Ingham, E. R. 1984. Rhizosphere bacterial population responses to root colonization by a vesicular-arbuscular mycorrhizal fungus. New Phytol. 96:555-563.
3. Azcon-G. de Aguilar, C., and Barea, J. M. 1978. Effects of interactions between different culture fractions of phospho-bacteria and Rhizobium on mycorrhizal infection, growth and nodulation of *Medicago sativa*. Can. J. Microbiol. 24:520-524.
4. Azcon R., Azcon-G. de Aguilar, C., and Barea, J. M. 1978. Effects of plant hormones present in bacterial cultures on the formation and responses to VA mycorrhiza. New Phytol. 80:359-364.
5. Bagyaraj, D. J. 1984. Biological interactions with VA mycorrhizal fungi. Pages 131-153 in: VA Mycorrhiza. C. L. Powell and D. J. Bagyaraj, eds. CRC Press, Boca Raton, FL. 234 pp.
6. Bagyaraj, D. J., and Menge, J. A. 1978. Interaction between a VA mycorrhiza and *Azotobacter* and their effects on rhizosphere microflora and plant growth. New Phytol. 80:567-573.
7. Barea, J. M., and Azcon-Aguilar, C. 1982. Production of plant growth-regulating substances by the vesicular-arbuscular mycorrhizal fungus *Glomus mosseae*. Appl. Environ. Microbiol. 43:810-813.
8. Barea, J. M., and Azcon-Aquilar, C. 1982. Interactions between mycorrhizal fungi and soil microorganisms. Pages 181-193 in: Les Mycorhizes: Biologie et Utilization. National Institute of Agronomic Research (INRA), France.
9. Barea, J. M., Bonis, A. F., and Olivares, J. 1983. Interactions between Azospirillum and VA mycorrhiza and their effects on growth and nutrition of maize and ryegrass. Soil Biol. Biochem. 15:705-709.
10. Bowen, G. D., and Theodorou, C. T. 1979. Interactions between bacteria and ectomycorrhizal fungi. Soil Biol. Biochem. 11:119-126.
11. Burr, T. J., and Caesar, A. 1983. Beneficial plant bacteria. Chemical Rubber Co. Crit. Rev. Plant Sci. 2:1-20.
12. Curl, E. A., and Truelove, B. 1986. The Rhizosphere. Springer-Verlag New York. 288 pp.
13. Davey, C. B. 1971. Nonpathogenic organisms associated with mycorrhizae. Pages 114-121 in: Mycorrhizae. E. Hacskaylo, ed. USDA Misc. Publ. 1189. 255 pp.
14. Dehne, H. W. 1982. Interaction between vesicular-arbuscular mycorrhizal fungi and plant pathogens. Phytopathology 72:1115-1119.
15. Forster, S. M., and Nicolson, T. H. 1981. Aggregation of sand from a maritime embryo sand dune by microorganisms and higher plants. Soil Biol. Biochem. 13:199-203.
16. Gilbert, R. G., and Linderman, R. G. 1971. Increased activity of soil microorganisms near sclerotia of *Sclerotium rolfsii* in soil. Can. J. Microbiol. 17:557-562.
17. Graham, J. H., Leonard, R. T., and Menge, J. A. 1981. Membrane mediated decrease in root exudation responsible for phosphorus inhibition of vesicular-arbuscular mycorrhiza formation. Plant Physiol. 68:548-552.
18. Graham, J. H., Linderman, R. G., and Menge, J. A. 1982. Development of external hyphae by different isolates of mycorrhizal *Glomus* spp. in relation to root colonization and growth of Troyer citrange. New Phytol. 91:183-189.
19. Hale, M. G., Moore, L. D., and Griffin, G. J. 1978. Root exudates and exudation. Pages 163-203 in: Interactions Between Non-Pathogenic Soil Microorganisms and Plants. Y. R. Dommergues and S. V. Krupa, eds. Elsevier Scientific Pub. Co., New York. 475 pp.
20. Hussain, A., and Vancura, V. 1970. Formation of biologically active substances by rhizosphere bacteria and their effect on plant growth. Microbiol. 15:468-478.
21. Katznelson, H. 1965. Nature and importance of the rhizosphere. Pages 187-209 in: Ecology of Soilborne Plant Pathogens: Prelude to Biological Control. K. F. Baker and W. C. Snyder, eds. Univ. of California Press, Berkeley. 571 pp.
22. Katznelson, H., Rouatt, J. W., and Peterson, E. A. 1962. The rhizosphere effect of mycorrhizal and nonmycorrhizal roots of yellow birch seedlings. Can J. Bot. 40:377-382.
23. Krishna, K. R., Balakrishna, A. N., and Bagyaraj, D. J. 1982. Interaction between a vesicular-arbuscular mycorrhizal fungus and *Streptomyces cinnamomeous* and their effects on finger millet. New Phytol. 92:401-405.
24. Li, C. Y., and Castellano, M. A. 1985. Nitrogen-fixing bacteria isolated from within sporocarps of three ectomycorrhizal fungi. Page 264 in: Proc. 6th N. Am. Conf. on Mycorrhizae, June 25-29, 1984, Bend, OR. 471 pp.
25. Linderman, R. G. 1986. Managing rhizosphere microorganisms in the production of horticultural crops. HortScience 21:1299-1302.
26. Linderman, R. G., and Call, C. A. 1977. Enhanced rooting of woody plant cuttings by mycorrhizal fungi. J. Am. Soc. Hortic. Sci. 102:629-632.
27. Malajczuk, N., and McComb, A. J. 1979. The microflora of unsuberized roots of *Eucalyptus calophylla* R. Br. and *Eucalyptus marginata* Donn. ex Sm. seedlings grown in soils suppressive and conducive to *Phytophthora cinnamomi* Rands. I. Rhizoplane bacteria, actinomycetes, and fungi. II. Mycorrhizal roots and associated microflora. Austr. J. Bot. 27:235-272.
28. Mayo, K., Davis, R. E., and Motta, J. 1986. Stimulation of germination of spores of *Glomus versiforme* by spore associated bacteria. Mycologia 78:426-431.
29. Meyer, J. R., and Linderman, R. G. 1986. Response of subterranean clover to dual inoculation with vesicular-arbuscular mycorrhizal fungi and a plant growth-promoting bacterium, *Pseudomonas putida*. Soil Biol. Biochem. 18:185-190.
30. Meyer, J. R., and Linderman, R. G. 1986. Selective influence on populations of rhizosphere or rhizoplane bacteria and actinomycetes by mycorrhizas formed by *Glomus fasciculatum*. Soil Biol. Biochem. 18:191-196.
31. Neal, J. L., Bollen, W. B., and Zale, B. 1964. Rhizosphere microflora associated with the mycorrhizae of Douglas-fir. Can. J. Microbiol. 10:259-265.
32. Neal, J. L., Jr., Lu, K. C., Bollen, W. B., and Trappe, J. M. 1968. A comparison of rhizosphere microfloras associated with mycorrhizae of red alder and Douglas-fir. Pages 57-71 in: Biology of Alder. J. M. Trappe, J. F. Franklin, R. F. Tarrant, and G. M. Hansen, eds. USDA For. Serv., Pac. Northwest For. Range Exp. Stn. 292 pp.
33. Oswald, E. T., and Ferchau, H. A. 1968. Bacterial associations of coniferous mycorrhizae. Plant Soil 28:187-192.
34. Parke, J. L., Linderman, R. G., and Black, C. H. 1983. The role of ectomycorrhizas in drought tolerance of Douglas-fir seedlings. New Phytol. 95:83-95.
35. Paul, E. A., Harris, D., and Fredeen, A. 1985. Carbon flow in mycorrhizal plant associations. Pages 165-169 in: Proc. 6th N. Am. Conf. on Mycorrhizae, June 25-29, 1984, Bend, OR. 471 pp.
36. Raj, J., Bagyaraj, D. J., and Manjunath, M. 1981. Influence of soil inoculation with vesicular-arbuscular mycorrhiza and a phosphate-dissolving bacterium on plant growth and ^{32}P-uptake. Soil Biol. Biochem. 13:105-108.
37. Rambelli, A. 1973. The rhizosphere of mycorrhizae. Pages 299-343 in: Ectomycorrhizae. G. L. Marks and T. T. Koslowski, eds. Academic Press, New York. 444 pp.
38. Ratnayake, M., Leonard, R. T., and Menge, J. A. 1978. Root exudation in relation to supply of phosphorus and its possible relevance to mycorrhizal formation. New Phytol. 81:543-552.
39. Rhodes, L. H., and Gerdemann, J. W. 1978. Translocation of calcium and phosphate by external hyphae of vesicular-arbuscular mycorrhiza. Soil Sci. 126:125-126
40. Rovira, A. D. 1985. Manipulation of the rhizosphere microflora to increase plant production. Pages 185-197 in: Reviews of Rural Science 6, Biotechnology and Recombinant DNA Technology in the Animal Production Industries. R. A. Leng, J. S. F. Barker, D. B. Adams, and K. J. Hutchinson, eds. University of New England, Armidale, NSW, Australia. 226 pp.
41. Safir, G. R., and Nelsen, C. E. 1985. VA mycorrhizas: plant and fungal water relations. Pages 161-164 in: Proc. 6th N. Amer. Conf. on Mycorrhizae, June 25-29, 1984, Bend, OR. 471 pp.

42. Schwab, S. M., Menge, J. A., and Leonard, R. T. 1983. Quantitative and qualitative effects of phosphorus on extracts and exudates of sudangrass roots in relation to vesicular-arbuscular mycorrhiza formation. Plant Physiol. 73:761-765.

43. Slankis, V. 1973. Hormonal relationships in mycorrhizal development. Pages 151-205 in: Ectomycorrhizae: Their Ecology and Physiology. G. C. Marks and T. T. Koslowski, eds. Academic Press, New York. 444 pp.

44. St. John, T. V., Hays, R. I., and Reid, C. P. P. 1983. Influence of a volatile compound on formation of vesicular-arbuscular mycorrhizas. Trans. Br. Mycol. Soc. 81:153-154.

45. Strzelczyk, E., and Pokojska-Burdziej, A. 1984. Production of auxins and gibberellin-like substances by mycorrhizal fungi, bacteria and actinomycetes isolated from soil and the mycorrhizosphere of pine (*Pinus sylvestris* L.). Plant Soil 81:185-195.

46. Subba Rao, N. S., Tilak, K. V. B. R., and Singh, C. S. 1985. Synergistic effect of vesicular-arbuscular mycorrhizas and *Azospirillum brasilense* on the growth of barley in pots. Soil Biol. Biochem. 17:119-121.

47. Sutton, J. C., and Sheppard, B. R. 1976. Aggregation of sand-dune soil by endomycorrhizal fungi. Can. J. Bot. 54:326-333.

48. Tilak, K. V. B. R 1985. Interaction of vesicular-arbuscular mycorrhizae and nitrogen fixers. Pages 219-226 in: Proc. Soil Biol. Symp., Hisar.

49. Tinker, P. B. 1984. The role of microorganisms in mediating and facilitating the uptake of plant nutrients from soil. Plant Soil 76:77-91.

50. Williams, P. G. 1981. The prospects of using vesicular arbuscular mycorrhiza in broadscale agriculture to improve the efficiency of phosphate fertiliser use. Rep. Aust. Meat Res. Counc. Workshop, Cambridge.