

AGROECOLOGIA, SOSTENIBILIDAD Y EDUCACION



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EFFECTS OF MICROBIAL INTERACTIONS IN THE MYCORRHIZOSPHERE ON PLANT GROWTH AND HEALTH

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EFFECTOS DE LAS INTERACCIONES MICROBIANAS DE LA MICORRIZOSFERA EN LA SALUD Y CRECIMIENTO VEGETAL

SUMMARY

Mycorrhizae induce changes in root exudation that alter microbial composition in rhizosphere soil. Soil microbes may also affect formation and function of mycorrhizae. Microbial interactions in the 'mycorrhizosphere' may affect growth and health of plants. Associations of specific bacteria with mycorrhizae can enhance plant growth due to mycorrhizal effects on the bacterial metabolism and function. For example, more bacterial N_2 fixation occurs on legumes colonized by compatible strains of VA mycorrhizal fungi than when colonized by no or incompatible strains. Inoculations with VA mycorrhizae and P-solubilizing bacteria enhance plant growth more than with either organism alone. Combinations of biocontrol agents and mycorrhizal fungi may increase biocontrol of soilborne pathogens. Agricultural practices may have decreased optimum combinations of mycorrhizae and their associates, and re-establishing such microbial associations may be necessary in an effort to have sustainable agriculture without excessive inputs of fertilizers and pesticides.

RESUMEN

Las micorrizas originan cambios en los exudados radicales, los cuales alteran la descomposición microbiana en la rizosfera del suelo. Del mismo modo, la microbiota del suelo puede también afectar la formación y función de las micorrizas. Las interacciones microbianas en la "micorrizosfera" pueden afectar el crecimiento y la salud de las plantas. Algunas asociaciones de bacterias específicas con las micorrizas pueden incrementar el

crecimiento vegetal debido a los efectos micorrízicos sobre el metabolismo y la función bacteriana. Por ejemplo, existen más bacterias fijadoras de nitrógeno, en las leguminosas colonizadas con cepas compatibles de hongos micorrízicos vesículo-arbusculares (V-A) que en aquellas colonizadas con cepas no compatibles o no colonizadas. La inoculación con micorriza V-A y con bacterias solubilizadoras de P incrementa el crecimiento vegetal en mayor grado que con un sólo organismo. Las combinaciones de los agentes de biocontrol y los hongos micorrízicos pueden incrementar el control biológico de los patógenos del suelo. Las prácticas agrícolas pueden haber disminuído las combinaciones óptimas de las micorrizas y los organismos asociados con ellas, y el restablecimiento de dichas asociaciones microbianas puede ser necesario, en un esfuerzo para tener agricultura sostenible sin entradas excesivas de fertilizantes y pesticidas.

SOIL MICROBES, PLANT GROWTH AND HEALTH, AND SUSTAINABLE AGRICULTURE

A sustainable agricultural system is one that, over the long term, (a) enhances environmental quality and the resource base on which agriculture depends, (b) provides for basic human food and fiber needs, (c) is economically viable, and (d) "enhances the quality of life for farmers and society as a whole" (American Society of Agronomy). The role of soil microorganisms in sustainable agriculture has been overlooked largely, and the role played by VA mycorrhizal (VAM) fungi in these processes has been, in my opinion, conspicuously overlooked (Mosse, 1986). The literature suggests that their role may be critical if agriculture is to return to the state where luxury levels of farm inputs of fertilizers, pesticides, and other chemicals are decreased to levels that are still economic, yet do not pollute the environment or pose health risks.

Rhizosphere soil organisms function in support of plant growth in a variety of ways, and loss in sustained productivity may be due to any one or more of those functions becoming limiting. In stable ecosystems, there is a consistent energy supply from plants that ensures the tight recycling of mineral nutrients and minimizes losses from the rhizosphere. When that plant input is altered by stresses or plant removal (harvest), and gradually the rhizosphere interactions and processes begin to fail, productivity declines. When that happens, farmers must compensate by fertilizer and pesticide inputs to maintain a sustained level of productivity.

Rhizosphere organisms are stimulated initially by the nutrient energy inputs from the plant as root exudates that favor some, not others. Among the groups of organisms that could affect plant growth are: (a) mycorrhizal fungi, (b) associative and symbiotic nitrogen fixers, (c) microbes that affect nutrient availability, (d) pathogens, (e) biocontrol agents/antagonists, (f) plant growth-promoting and deleterious rhizobacteria, (g) arthropods, nematodes, and protozoa that graze on bacteria and fungi, and (h) other rhizobacteria that

produce growth regulating substances. Mycorrhizae play a pivotal role in the establishment, maintenance and function of many of these microbes. The purpose of this paper is to discuss the interactions between VA mycorrhizal fungi and other rhizosphere occupants, and link those microbial interactions to plant growth and health and to emerging concepts of sustainable agriculture.

MYCORRHIZAE AND THE MYCORRHIZOSPHERE

In nearly all ecosystems, the coupling of plants with rhizosphere microbial processes is optimized by mycorrhizal fungi. These fungi form a symbiotic relationship with plant roots, and the fungal symbiont becomes a major interface or connection between the soil and plant. Mycorrhizal fungal hyphae extend from the root out into the soil where they interface with soil particles and function as absorptive structures for mineral elements and water. Extraradical hyphae also attract other microbes, and together they form water stable aggregates necessary for good soil tilth. Mycorrhiza formation causes little change in root morphology, but significant physiological changes in the host plant that make the mycorrhizal plant grow and respond to environmental stresses differently from a non-mycorrhizal plant. For example, mycorrhizal plants exhibit changes in concentrations of growth regulating compounds such as auxins, cytokinins, and gibberellins. Photosynthetic rates increase, and the partitioning of photosynthate to shoots and roots changes. The nutritional status of the host tissues changes in response to altered uptake of minerals from the soil, and this in turn can change structural and biochemical aspects of root cells that can alter membrane permeability and thus the quality and quantity of root exudation. Altered exudation induces changes in the composition of microorganisms in the rhizosphere soil, now appropriately called the "mycorrhizosphere" (Rambelli, 1973; Linderman, 1988).

Mycorrhizae could have direct interactions with other soil organisms, or they could influence those organisms indirectly by changing host plant physiology. The concept of the mycorrhizosphere implies that mycorrhizae significantly influence the microflora of the rhizosphere. Analysis of rhizosphere soil of non VAM plants compared to micorrhizosphere of VAM plants clearly has demonstrated selective, qualitative changes in microbial populations therein (Bagyaraj and Menege, 1978; Ames *et al.*, 1984; Meyer and Linderman, 1986b; Secilia and Bagyaraj, 1987). Such changes include many microbial groups known to influence plant growth and health, but only nitrogen fixing bacteria, microbes that affect nutrient availability, and microbes that suppress root diseases will be discussed here.

BIOLOGICAL NITROGEN FIXATION

Sustainable agriculture should place more reliance on biological N_2 fixation to reduce fertilizer inputs. VAM fungi do not fix atmospheric N_2 , but they definitely enhance N_2

fixation by nodule-producing bacteria, and positively interact with free-living or associative nitrogen-fixing bacteria. The mechanisms of such enhancement are still unclear, however (Bethlenfalvai, 1992; Barea *et al.*, 1992).

Most leguminous plants have a dual symbiosis with both nodule-forming *Rhizobium* and VAM fungi. With both symbionts present, plant growth is generally much greater than for plants symbiotic with either alone. Many reports indicate that greater growth is due to mycorrhizae increasing P nutrition which would favor N_2 fixation by *Rhizobium* nodules. Others have challenged that notion by demonstrating non-P-mediated effects of VAM on nodule formation and N_2 fixing activity (Asimi *et al.*, 1980; Ames and Bethlenfalvai, 1987; Lanson and Linderman, 1991). Generally, mycorrhiza formation increases the number of nodules formed by *Rhizobium* (Smith *et al.*, 1979) as well as their size and N_2 -fixing activity (Pacovsky *et al.*, 1986). Some VAM fungi effectively stimulate nodulation, while others do not (Lanson and Linderman, 1991). Microbial changes in the mycorrhizosphere could also affect competition, favoring *Rhizobium* over other rhizobacteria (Grimes and Mount, 1984; Meyer and Linderman, 1986a). Mycorrhizae could also increase the uptake of nutrients other than P, such as Cu and Zn that are essential for N_2 fixation (Pacovsky, 1986), or NH_4 and NO_3 sources of N (Ames *et al.*, 1983; Smith *et al.*, 1985; Barea *et al.*, 1987).

It is apparent that nearly all legumes with *Rhizobium* nodules grow better if they are also mycorrhizal. As with other VAM situations, the plant and the *Rhizobium* system benefit from the presence of VAM by the correction of any deficiency which is limiting the system. Those deficiencies could be P or other nutrients, but other direct or indirect mechanisms also could be operational. If not all VAM isolates interact the same with *Rhizobium* in a given soil, the biological nitrogen fixation may not be maximum. Disturbance of agricultural soils may even minimize the involvement of any VAM fungi in the *Rhizobium* system. All the components of the tripartite system must function optimally for maximum plant growth to occur. The *Rhizobium*-VAM partnership nearly always exists, but many not necessarily be optimized with the best combination of symbionts for the host species. The challenge of sustainable agriculture encourages the characterization of each tripartite relationship and optimization of all components so that they function compatibly and in concert.

Some free living diazotrophic bacteria fix atmospheric N_2 , and some positively interact with mycorrhizae. When these bacteria, such as species of *Azospirillum* or *Azotobacter*, are combined with VAM fungi, growth of the inoculated crops may be increased, but the mechanism responsible is controversial since increases sometimes occur without evidence of increased N_2 fixation or increased N content in the plants (Tilak and Singh, 1988; Barea *et al.*, 1983; Pacovsky *et al.*, 1985). Some suggest that these bacteria produce plant hormones that account for increased plant growth (Azcon and Barea, 1975; Tien *et al.*, 1979; Barea and Azcon-Aguilar, 1982), or that they enhance root growth and thereby increase the nutrient absorption capacity and the chance of plants avoiding drought stress (Kapulnik *et al.*, 1987). Some of these bacteria occur closely associated with VAM fungal spores or

VAM roots (Tilak *et al.*, 1987a and b), suggesting a close spatial association wherein the bacteria might utilize P and C from the VAM, and the VAM fungi might transport fixed nitrogen from the bacteria to the plant. Furthermore, their isolation from the root cortex (Tilak and Subba Rao, 1987) opens the possibility of a direct linkage between the two organisms within the plant tissues.

BACTERIA THAT INCREASE NUTRIENT AVAILABILITY

Synergistic interaction between mycorrhizae and phosphate solubilizing bacteria (PSB) (*Pseudomonas* and *Agrobacterium* spp.) has been shown (Barea *et al.*, 1975; Azcon *et al.*, 1978; Delorenzini *et al.*, 1979; Azcon-Aguilar and Barea, 1978; Krone *et al.*, 1987; Raj *et al.*, 1981), as indicated by increased weight, N and P levels, and increased VAM root colonization, but some confusion exists as to whether growth increases are due to increased availability of P solubilized by the PSB, or to some other mechanisms such as the production of plant hormones or vitamins by PSB. PSB occur more frequently in the rhizosphere than nonrhizosphere soil, and a high proportion of them produce IAA, gibberellins, and cytokinins (Barea *et al.*, 1976) or vitamins (Baya *et al.*, 1981). Dodd *et al.* (1987) showed that acid phosphatase activity around mycorrhizae of wheat (*Triticum aestivum* L.) and onion (*Allium cepa* L.) increased with corresponding increases in shoot dry weight and tissue P content, suggesting that the numbers and activity of phosphatase producing microbes might be enhanced by VAM, as suggested earlier by Krishna and Bagyaraj (1985).

Nutrients in the mycorrhizosphere soil are utilized and converted by rhizobacteria. Secilia and Bagyaraj (1987) demonstrated increased numbers of urea- and starch-hydrolyzing bacteria in mycorrhizosphere soil compared to rhizosphere soil of non VAM guinea grass plants. Others (Linderman and Marlow, unpublished results) have demonstrated that some rhizobacteria are able to degrade protein or amino acid substrates and produce excess NH_3 which could be available for plant uptake in the NH_4^+ form.

Plant-growth promoting rhizobacteria (PGPR) inhabit the rhizosphere, and can enhance growth (Burr and Caesar, 1984), either by producing antibiotics or siderophores that suppress deleterious microbes (Schippers *et al.*, 1987), or by producing phytohormones or other growth-enhancing compounds that directly affect the plant (Brown, 1974), or by somehow enhancing the nutritional status of the plants. PGPR may also interact with mycorrhizal fungi in some way, perhaps because they are closely associated in or on plant roots. Meyer and Linderman (1986a) tested the interaction between the PGPR, *Pseudomonas putida*, and VA mycorrhizae on subclover, and demonstrated a growth enhancement and corresponding increased nutrient content when both organisms were used, compared to each alone.

INTERACTIONS WITH ROOT PATHOGENS

The premise of sustainable agriculture that production inputs should be reduced without significant loss of productivity includes reduction of biocides used to control diseases and insect pests. Diseases can be controlled by manipulation of resident microbes or by introducing antagonists to reduce the amount of inoculum or disease producing activity of a pathogens (Baker and Cook, 1974; Cook and Baker, 1983). Reviews on biocontrol usually neglect the role played by mycorrhizal fungi. The low level of root diseases in natural, undisturbed ecosystems without pesticidal inputs, compared to the relatively high disease incidence that would occur in agroecosystems without the use of pesticides, leads one to question what was lost in the conversion from undisturbed to disturbed systems. One obvious answer is the change in rhizosphere microbes, especially VAM fungi and their bacterial associates. If the kinds of VAM fungi and/or the extent of their colonization of roots has changed as a result of intensive agricultural practices, then the balanced, effective mycorrhizosphere microbes of the undisturbed ecosystems could have been rendered ineffective.

Since VA mycorrhizae are major components of the rhizospheres of plants, it is logical that they could affect the incidence and severity of root diseases. The subject has been reviewed (Schenck and Keilam, 1978; Schonbeck, 1979; Dehne, 1982; Hussey and Roncadori, 1982; Ingham, 1988; Schenck, 1989; Caron, 1989; Jalali and Jalali, 1991), but there is still controversy. The reports are many and mixed, with many indicating reduced disease due to VAM, but some indicating no effect on disease, and others indicating increased disease severity. Drawing any conclusions is difficult, partly because so many different pathogens and diseases have been involved, and partly because of the experimental conditions of each study. Clearly, one should expect varied results, even if the VAM fungi used had been the same (Schenck, 1989).

I believe that VA mycorrhizae can contribute to root disease suppression in a number of ways, and thus contribute to sustainable agriculture. A number of mechanisms for disease reduction are possible, such as: (a) improved host nutrition resulting in more vigorously growing plants better able to ward off or tolerate root disease and other environmental stresses, such as drought, that could predispose them to greater fungal pathogen infections; (b) enhanced plant defence mechanisms; and (c) enhanced protective rhizosphere microbes.

The evidence to support the mechanism of enhanced plant health by improved nutrition comes from experiments where VAM effects were mimicked by fertilizer P (Davis *et al.*, 1979; Davis, 1980; Graham and Menge, 1982; Graham and Egel, 1988). On the other hand, Caron *et al.*, (1986a, b, c) showed that root disease on tomato caused by *Fusarium oxysporum* f. sp. *radicis-hypocypersici* and population levels of the pathogen in rhizosphere soil of non VAM plants were not reduced by additional P fertilizer, but they were with VAM plants, even though plant growth and tissue P were not affected. This work suggests the

involvement of some other mechanism of disease suppression other than enhanced P uptake.

Localized morphological effects have been shown to occur in VAM roots, such as increased lignification of tomato and cucumber root cells of the endodermis which reduced *Fusarium* wilt (Dehne and Schönbeck, 1979), pink root of onion (Becker, 1976), and *Thielaviopsis* black root rot of VAM holly plants (Wick and Moore, 1984).

Physiological changes induced by VAM also have been reported to be involved in suppression of root pathogens. Increased anti-fungal chitinase and agrinine accumulation in VAM roots was suggested to explain suppressed *Thielaviopsis* sporulation (Baltruschat and Schönbeck, 1975; Dehne *et al.*, 1978). Elevated levels of phytoalexin-like isoflavanoid compounds in VAM plants have also been reported (Morandi *et al.*, 1984). Physiological effects could be localized or systemic as was shown on *Aphanomyces* root rot of peas which was only suppressed by VAM when the two organisms were on the same roots (Rosendahl, 1985); a similar response occurred on *Phytophthora* root rot of citrus (Davis and Menge, 1980).

When VA mycorrhizae are reported to suppress root disease, they generally were established and functioning before invasion by the pathogen. This has been demonstrated by Stewart and Pflieger (1977) on *Pythium* and *Rhizoctonia* root rot of poinsettia, by Bartschi *et al.*, (1981) on *Phytophthora* root rot of Lawson cypress (*Chamaecyparis lawsoniana* (A. Murr.) Parl., and by Rosendahl (1985) with *Aphanomyces* root rot of pea (*Pisum sativum* L.). That this would be the case seems logical considering both the faster infection rate of most fungal root pathogens, compared to VAM fungi, and the time needed for VAM effects on the host physiology to occur. Furthermore, other reports have indicated that established root infections by various pathogens can reduce colonization by VAM fungi and therefore the potential for positive effects on disease incidence or severity (Alek and Menge, 1990). Sometimes, however, root pathogens and VAM fungi occupy adjacent tissues in roots without any apparent effects on each other (Schönbeck, 1979; Dehne, 1982).

While any of the above mechanisms, or combinations thereof, could be involved in VAM suppression of root diseases, one that should be considered more carefully is the VAM alteration of rhizosphere populations of antagonists. Even though the evidence is clear that such shifts could and do occur (Meyer and Linderman, 1986b; Secilia and Bagyaraj, 1987), most studies have not considered these changes, so relatively little data is available that supports the hypothesis. Meyer and Linderman (1986b) showed that microbial suppression of *Phytophthora* sporangium production occurred in mycorrhizosphere soil, compared to rhizosphere soil of non VAM plants, and studies by Caron *et al.* (1985, 1986a, b, c) indicated a reduction in *Fusarium* populations in tomato mycorrhizosphere soil, possible due to increased antagonists therein. While not considered by the authors, the results of Bartschi *et al.* (1981), indicating protection of cypress roots against *P. cinnamomi*

when plants were pre-inoculated with VAM pot-culture inoculum, could have been explained on the basis of the time needed to increase the level of antagonists. They used a mixture of VAM fungi grown in pot cultures where antagonists could have been selected (Secilia and Bagyaraj, 1987).

If VAM formation favors the increase of antagonists against root pathogens, then agricultural disturbance that decreases VAM could also reduce the levels of antagonists, and that in turn could account for increased disease requiring inputs of fungicides. Reversing the process, therefore, could contribute to sustainable agriculture and allow for reduction in fungicide use. To guard against the chance that compatible combinations of VAM and antagonists occur in the same soil or growth medium, growers could inoculate seeds or transplants with them to guarantee their early establishment on the roots prior to pathogen invasion (Linderman, 1988, 1991). The possibility that antagonistic rhizosphere bacteria or fungi might inhibit mycorrhizal fungi and thereby reduce their effectiveness (Krishna *et al.*, 1982) has been evaluated extensively by Linderman *et al.* (1991) who found and others (Meyer and Linderman, 1986a; Paulitz and Linderman, 1989, 1991b; Linderman *et al.*, 1991; Millner *et al.*, 1990) who found little or no adverse effects of the biocontrol agents on establishment and function of VA mycorrhizae. These results indicate that VAM fungi are relatively tolerant of antagonists that inhibit fungal pathogens by one or more mechanisms, and that VAM fungi, having evolved with plants, are highly rhizosphere-competent and are compatible with such antagonists and even function in concert with them.

CONCLUSIONS

With few exceptions, crop plant roots have mycorrhizal associations, and most have VA mycorrhizae. The degree of colonization of roots by VAM fungi and thus the effects of the symbiosis may vary, depending on the total interaction between host, symbiont, and environment. In most cases, the evidence is strong that VA mycorrhizae significantly change the host physiology, causing changed root exudation, resulting in a new microbial balance in the mycorrhizosphere. The interactions that occur in the mycorrhizosphere can profoundly affect plant growth and health.

Since plants have undoubtedly co-evolved with mycorrhizal fungi, it is logical that other microbes could have evolved along with the mycorrhizal fungi. We have only begun to appreciate that microbial associations with plant roots and with each other is normal in natural ecosystems. In disturbed situations, such as the agroecosystem, sustained crop productivity is now only possible with considerable inputs to compensate for the effects of the disturbance. Sustained plant growth occurs in natural ecosystems because of the balance that has developed over evolutionary time, a balance between the host plants, their microbial associates, and the macroenvironment. Disturbance to that balance decreases any

chance for sustainability without inputs. Reconstruction should begin with the establishment of appropriate populations of mycorrhizal fungi and as many of their beneficial associates as possible. Mycorrhizal fungi should be placed to cause early colonization, along with fungal and bacterial biocontrol agents with rhizosphere competence and compatibility with their mycorrhizal associates. While the utility of such combinations has not been demonstrated, the logic of their use as a crop management strategy in sustainable agriculture is apparent.

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