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117 The Mycorrhizosphere in Plant and Soil Nutrition

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Introduction

The mycorrhiza, or fungus-root, is a symbiotic association formed by the roots of the host plant and its endophyte, a soil fungus. The term "mycorrhiza" is overly restrictive, for it reflects only the relationship between the endophyte and the host plant. Vesicular-arbuscular mycorrhizal (VAM) fungi, which colonize crop and forage plants, have equally important interactions with the soil. Their extraradical mycelia form a loose network of hyphae around roots which extends into the surrounding soil by several centimeters. There, in the "bulk soil," the fungus enters into a second symbiotic association with the biotic component of the soil. The site where the interactions between VAM fungi and the soil biota take place has been called the mycorrhizosphere (Davey, 1971). The permeation of the bulk soil by this fungal extension of the root system broadens the spatial limits and the concept of the rhizosphere (Curl and Truelove, 1986), for the biological and chemical reactions and exchanges concentrated in the rhizosphere (3 mm around the root) of non-VAM plants may be mediated by VAM-fungal hyphae up to 8 cm away from the root (Rhodes and Gerdeman, 1975).

The symbiotic exchanges between VAM-fungi and the biota of soil microsites not reached by roots are taking on a new significance in an agricultural research environment increasingly dominated by the imperatives of soil and water conservation (CAST, 1982). The fungus-mediated transport of plant metabolites to the bulk soil (mycorrhizosphere) has been shown to act as a mechanism for soil structure formation (Thomas et al., 1986). The role of VAM fungi in the plant-soil system is not limited to that of plant nutrition, but extends to soil nutrition, by means of a two-way flow of nutrients from soil to plant and from plant to soil.

Mycorrhizae in Agroecology

Soils typically contain the propagules of more than one species of VAM fungus. Evolved primarily for survival and for compatibility with the existing biotic and abiotic soil conditions and the native flora (Bowen, 1980), any shift in conditions, such as the introduction of exotic plants, cultivation, and agricultural chemicals is likely to alter the composition and effectiveness of VAM flora (Howeler et al., 1987). The results may not be discernible in terms of crop production under modern fertilizer regimes, but hidden effects of disturbing the balances which permit the plant-VAM fungus-soil continuum to function in concert will accumulate. These hidden VAM effects are under intense study. They include plant resistance to pests (Dehne, 1982) and stress (Safir, 1987), the abundance and composition of the soil microflora (Curl and Truelove, 1986), soil structure (Oades, 1984), and nutrient-use efficiency (Bethlenfalvay et al., 1987). The search for a "best" VAM fungus for high crop productivity with a minimum of soil loss is beginning to reveal that this best fungus is probably a combination of fungi, each most suited to perform different functions within the range of symbiotic requirements.

Plant Nutrition

Uptake of Minerals from the Soil

The provision of P by VAM fungi to host plants growing in P-deficient soils is so well known that it is often thought of as the "VAM effect". Since root colonization by VAM fungi of severely P-deficient plants has similar effects on the host as does P fertilization, the fungus has even been called a biological fertilizer. The resulting relief from P stress can have dramatic effects on plant growth, development, and function. However, since the uptake of other mineral nutrients and effects on other symbiotic organisms are also involved, an integrated approach to the study of mycorrhiza in plant-soil nutrient dynamics is necessary (Ames and Bethlenfalvay, 1987).

Nutrient Transfer Between Plants

Plant-to-plant nutritional interactions may follow two pathways. One is the soil-pool pathway (Newman and Ritz, 1986), in which organic compounds are released from one plant into the soil and taken up by another following degradation and mineralization. Another, direct transfer pathway also exists and is mediated by live VAM-fungal hyphae which connect the roots of plants. Such transfer has been demonstrated for P, C, and N and for water in ectomycorrhizae. Direct nutrient transfer occurs in both inter- and intra-specific plant combinations. Its implications for plant-plant interactions are profound (Fitter, 1985) and may be an important mechanism affecting the ecology of intercropping systems and weed-crop relationships (Allen, 1988).

Soil Nutrition

Carbon Flux to the Soil

An important sink for atmospheric C converted to organic compounds by photosynthesis is the soil (Oades, 1984). Carbon lost by the plant may represent a considerable percentage of total net fixed C (Whipps and Lynch, 1986). Among the diverse compounds gained by the soil (Bowen, 1980), the water-soluble exudates are of particular interest because of their dual role in serving as a substrate for the soil microbiota and in the solubilization and chelation of nutrients for direct uptake by the roots. The production of root exudates is apparently inhibited to some extent by VAM colonization (Cooper, 1984). Such losses of C flux to the soil may be compensated by the production of extraradical mycelia. The rapid turnover of VAM-fungal mycelia could make them a more abundant microbial growth substrate in the bulk soil than root exudates since the zone of influence of the latter is diffusion-limited (Whipps and Lynch, 1986).

Soil Aggregation

An interruption of the flux of C to the soil generally results in the loss of soil structure (Lynch, 1986). Fallowing, in particular, has been shown to lead to disaggregation connected to a decline in mycorrhizae and to nutritional disorders (Thompson, 1987). Early insights into the role of VAM fungi in soil aggregation (Lynch, 1986; Thomas et al., 1986) suggest their future utilization in erosion control. Of particular interest in this context are the nutritional interactions between filamentous, chitin-decomposing actinomyces, and VAM fungi (Ames et al., 1988) because of the role of the former in stabilizing soil microaggregates.

Plant Stress

Plants are under stress when the optimal expression of their genetic potential for growth, development, and reproduction is inhibited by adverse conditions. The incompatibility of high potential yield with high resistance to stress (Vanderplank, 1984) places priority on investigations of stress in agricultural research. Mycorrhizae will play an increasing role in this work since they are now being recognized as natural agents of biological plant protection and stress reduction (Schonbeck, 1987).

Nutrient Deficiency, Toxicity, and Use Efficiency

The improvement of plant nutrition by VAM fungi in deficient soil is due to the capacity of their extraradical hyphae to extend the uptake surface of the root system and to absorb poorly mobile nutrient ions efficiently (Cress et al., 1979). Extraradical mycelia are probably produced at a much lower cost to the symbiotic association than root growth. While the fungus may be a large C drain on the host under certain conditions (parasitism), the mutual cost-benefit ratios are usually in favor of both symbionts (Bethlenfalvay et al., 1983).

Mycorrhizal fungi have been found to alleviate heavy metal toxicity (Gildon and Tinker, 1983). The proposed mechanisms range from immobilization in the fungus to effects on the availability of metals in the soil. In addition to efficiencies in the uptake or exclusion of nutrients by mycorrhizae, a more efficient utilization of P and N within VAM plants has recently been reported, based on comparisons of VAM plants and nutritionally equivalent controls (Bethlenfalvay et al., 1987).

Drought, Pests, and Pesticides

The influence of VAM fungi on plant water status is an area of intense research interest whose insights may have far-reaching effects in agricultural practice (Safir, 1987; Trappe, 1981). While the mechanism of water uptake by the VA mycorrhiza is still controversial, its stimulatory effects on leaf gas exchange have been demonstrated (Bethlenfalvay et al., 1987).

Few areas in mycorrhizal research are as fragmentary as the literature on interactions of the fungi with other organisms and with the unintentional effects of pest-control chemicals. While the effects of VAM colonization on plant disease are generally positive (Dehne, 1982), the influence of pesticides on non-target organisms, and, therefore, on crop productivity, can be unforeseen and profoundly negative (Trappe et al., 1984).

Summary

Much of the mycorrhizal message was summarized by Howard (1948) 40 years ago: "The presence of an effective mycorrhizal symbiosis is an essential requisite for plant health." Can we, 40 years later, extend this verdict to apply to soil health as well? The jury is still out on this. But evidence is accumulating that the role of the mycorrhizal fungus as a soil symbiont is equal to its influence on the plant as an endophyte, and that this dual role goes beyond that of bidirectional nutrient transfer.

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