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Agro-ecological aspects of the mycorrhizal, nitrogen-fixing legume symbiosis

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Abstract

Vesicular-arbuscular mycorrhizal (VAM) fungi have fundamental effects on the ecophysiology of nodulated legumes, on the biota of the surrounding soil and on associated non-legumes. The effects are seen to be mediated through the direct transfer of nutrients from plant to plant by live hyphae of the soil mycelium, and through improving the competitiveness of legumes in nutrient uptake. As envisioned, the main role of legumes, in the open source-sink system between associated plants and the soil biota, is that of a nitrogen source. The export of nitrogen may be balanced by flows of carbon and phosphorus from plant to plant along gradients of sink demand. Soil microbes are beneficiaries of inter-plant nutrient transport, utilizing exudates as well as the soil mycelium as substrates, while the products of microbial metabolism serve to aggregate the abiotic component of the soil. Thus, the tripartite legume association is seen to function not only as a self-contained system, but as one involved in nutrient fluxes between adjacent plants and the soil that surrounds its roots.

Introduction

Following a lag phase in research on the tripartite association between legumes, rhizobia and vesicular-arbuscular mycorrhizal (VAM) fungi (Asai, 1944; Jones, 1924; Stahl, 1900), evidence for a synergistic relationship between the endophytes (see Mosse, 1977) has led to a mushrooming in interest. The findings on N_2-fixing VAM legumes were presented in detail by Barea and Azcón-Aguilar (1983), and excellent reviews on the ecology (Allen and Allen, 1989), physiology (Smith and Gianinazzi-Pearson, 1988) and ecophysiology (Safir, 1987) of the VAM symbiosis and on progress in N_2-fixation research (Bothe *et al.*, 1988) in general are also available. We will therefore not summarize information already available, but will focus on the changes in perception of the role and rationale for the tripartite VAM association in the agro-ecosystem.

Changing concepts

Since first described a century ago (Frank, 1885), the mycorrhiza (fungus-root) was considered to be a plant symbiosis, whose obligately biotrophic VAM-fungal component formed an integral part of the plant (Gianinazzi *et al.*, 1982). Focus on the plant was expressed even by the choice of terms describing fungal organs: the mycelia are called intra- or extraradical, and the vast majority of the literature describes VAM effects on plants only. While this aspect will no doubt remain important, changing agricultural priorities (Paul *et al.*, 1985) are re-focussing the role of VAM fungi as key components of the rhizosphere ecosystem (Linderman, 1988a). This process has gained additional impetus during the past decade as a result of findings which demonstrated the influence of VAM fungi both on the microbiota of the bulk soil (see Linderman, 1988b) and on adjacent plants due to inter-plant linkages formed by the live VAM-fungal hyphae of the soil mycelium (Newman, 1988). Thus, we are coming to view the VAM fungus as a soil symbiont as well as a plant symbiont, but more importantly, also as an interface between plant and soil communities.

Mycorrhizae: agents of plant cooperation

The symplastic mycorrhizal connections between plants have special significance for the tripartite legume association because of the latter's role as a source of N (Barea *et al.*, 1987) to the associated soil ecosystem. Traditionally, the transfer of N from a legume to its environment was thought to occur only by the 'soil-pool pathway' (*sensu* Newman and Ritz, 1986) through the eventual mineralization of N-rich legume biomass. By contrast, the 'direct transfer pathway' of nutrients from plant to plant by VAM-fungi provides for the immediate export of N (van Kessel *et al.*, 1985) and C (Francis and Reed, 1984) to adjacent plants. The resulting open source-sink system between plants of varying N- and C-reduction capabilities and requirements would conceptually extend the influence of the tripartite legume association to associated non-legumes, and also to the organisms of the surrounding soil ecosystem which are in trophic interchange with the VAM soil mycelium (Bagyaraj, 1984). While the evidence on mycorrhizal linkages and their possible roles is still tentative (Newman, 1988), the implications for plant to plant interactions are profound (Fitter, 1985).

When grown in nutrient-deficient substrates, the fungal, rhizobial and plant components of the tripartite association may be regarded as the sources of P, N, and C, respectively, and as sinks for the products of their co-symbionts (Bayne *et al.*, 1984). In the restricted, intra-plant system, the acquisition and incorporation of nutrients is determined largely by source and sink limitations. In the expanded, VAM-linked, inter-plant system, such source-sink relationships are likely to be influenced by differential P-uptake and CO_2-fixation capabilities and utilization requirements, as influenced by differences in the mycotrophic status (Trappe, 1987) of the associated plants. Transfer of P (Newman and Ritz, 1986) has been demonstrated and the potential effects of inter-plant fluxes of P and C on N_2 fixation may be inferred from the well-known effects within the intra-plant symbiosis (Brown and Bethlenfalvay, 1987).

Our appreciation of the impact of VAM-mediated nutrient transfer on agriculture is limited at present, since the literature of multiple cropping systems (Francis, 1986) and that of legume crops (Wilcox, 1987) has taken little note, if any, of the existence of mycorrhizae. Gains to non-legumes, as well as legumes, in intercrop systems are thought to be due to different competitive situations (Haynes, 1980) of which the ecology of weeds and their mycorrhizal status (Trappe, 1987) is perhaps the least understood. Conflicting data on benefits to non-legumes from N supplied by an intercropped legume (see van Kessel and Roskoski, 1988; Abaido and van Kessel, 1989) may be resolved as inter-plant VAM effects on factors affecting N_2 fixation, such as soil N availability (Morris and Weaver, 1987), P nutrition (Barea *et al.*, 1987) and CO_2 fixation (Brown *et al.*, 1988; Sheehy, 1987) become better known.

Mycorrhizae: agents of plant competition

The effectiveness of VAM fungi in enhancing plant growth is dependent on fungal, plant and soil factors (Bethlenfalvay *et al.*, 1985b; Sainz and Arines, 1988). Plant species and cultivars within species differ in their dependence on the fungi (Reeves, 1987). While symbiotic plant response may vary with fungal species and even with edaphotypes of the same morphospecies (Bethlenfalvay *et al.*, 1989), plants most dependent on mycorrhizae are those with coarse roots and few root hairs (Howeler *et al.*, 1987; Mosse, 1981). Plants best able to extract limiting nutrients in marginal soils have a competitive advantage (Mosse, 1977). Thus, legumes with less extensive root systems are less efficient nutrient absorbers than grasses (Haynes, 1980), and may show large responses to VAM colonization (see Abbott and Robson, 1984a). Legumes can be highly dependent on colonization by native VAM fungi (Sainz and Arines, 1988), but enhanced growth responses to more effective introduced fungi have also been observed (see Hall, 1987). The co-evolution of plants with their VAM-fungal endophytes over geological time (see Trappe, 1987) would have favored the establishment of best-adapted host-endophyte combinations in natural habitats. Recent cultural disturbances of soils are often detrimental to VAM fungi (tillage, Evans and Miller, 1988; chemicals, Trappe *et al.*, 1984) and the introduction of exotic crop plants make the indigenous VAM fungi poorly suited for the new conditions (Hall, 1984) and agricultural requirements (Hayman, 1987).

The data on VAM influence on inter-plant competition (Allen and Allen, 1989; Safir, 1987) raise the question whether the cooperative and competitive VAM effects on plant-to-plant interactions may be counteractive. The answer is likely to be particularly complex for legumes, because of the complexity of the tripartite association (Daft *et al.*, 1985) both as a strong sink for P and a source of N. Thus, when the N source (legume) is out-competed for P, the resulting inhibition of N_2 fixation will be felt by the successful competitor (non-legume) as N stress, to the detriment of both. This simple scenario is in reality complicated by differences in plant-fungus preferences (Louis and Lim, 1988), inter-fungal competition (Abbott and Robson, 1984b), and antagonistic (Bayne and Bethlenfalvay, 1987; Bethlenfalvay *et al.*, 1985a) or stimulatory (Dagoberto, 1986) effects between VAM fungi and rhizobia in the legume. Soil effects (Hayman, 1982) and differences in the production of reduced C, and its allocation within and among associated plants and its loss to (gain by) the soil (Oades, 1984; Francis and Read, 1984; Paul and Clark, 1988) add a further little-known dimension to the role of VAM fungi in plant competition.

Recent reports of adverse effects of disturbance of VAM mycelial systems (Read and Birch, 1988) on plant growth and nutrition add further credence to the role of fungal hyphae in nutrient transfer. Should future work establish the cooperative model as a significant mechanism to supplement the competitive model in plant-to-plant interactions, it will probably also provide another reason for the common occurrence of multiple VAM colonization: the many desirable properties of the one 'ideal endophyte' (Daft, 1983), which are probably distributed among the several actual (less than ideal) ones, would have to include differential, bi-directional nutrient-transfer capabilities.

Mycorrhizae: agents of soil nutrition

The effectiveness of VAM fungi and rhizobia as legume symbionts has been measured in terms of host-plant development (Barea and Azcón-Aguilar, 1983) characteristic of production-oriented agriculture. With the shift in priorities in the 1980s to productivity and resource conservation (Gibbs and Carlson, 1985; Healey *et al.*, 1986), the soil, and the dynamics of its biotic component (Curl and Truelove, 1986) may become additional focal points for research on the legume association. Since the soil mycelium of VAM fungi represents a significant portion of the soil microbial biomass (Hayman, 1978), and since the cell walls of its hyphae are composed mainly of the amino-sugar chitin (Weijman and Meuzelaar, 1978), the soil hyphae of legume mycorrhizae may be one of the most important vehicles for C and N input into the soil. We therefore expect soil organic matter content and, as a consequence, aggregate stability (Lynch and Bragg, 1984; Oades, 1984) to become new measures of VAM effectiveness, complementing that of plant response.

The literature of VAM effects on soil aggregation is brief and had been recently reviewed by Thomas *et al.* (1986), who found a highly significant (60%) increase in water-stable aggregate formation in VAM soil (onions) and disaggregation in nonVAM controls over a five-month growth period. In VAM legumes (Phaseolus), Sutton and Sheppard (1976) showed that the binding of sand to extensive VAM-fungal mycelia was the mechanism of linking sand grains in aggregates, and isolated an adhesive polysaccharide as the binding agent (Clough and Sutton, 1978). Such adhesion of soil particles to fungal hyphae may have important consequencs for soil stabilization (Lynch and Bragg, 1984). It provides sites where microorganisms flourish (Linderman, 1988b) and where their organic products contribute to the formation of aggregates at different levels of size and organization (Gupta and Geminda, 1988; Tisdall and Oades, 1982). While each organism may have a necessary function in the aggregation process, fungi and filamentous actimomycetes (streptomyces) were shown to be most effective and rhizobia were intermediate in binding soil particles into crumbs (Harris *et al.*, 1966). Of these, the largest (>2 mm) are considered to be fungal products, while the actinomycete-produced crumbs are slightly smaller (Focht and Martin, 1979).

The interest in actinomycetes, as important 'outsiders' of the legume association, is based not only on their role in soil aggregation. As chitin decomposers, they are associated with VAM fungi (Meyer and Linderman, 1986), producing both antagonistic (Krishna and Bagyaraj, 1982) and positive (Mugnier and Mosse, 1987) effects. Recently, the closeness of the actinomycete-VAM fungus association had been emphasized by Ames *et al.* (1989) who showed that 82% of 190 spores of a VAM fungus were colonized by actinomycetes. Using selected strains from his isolates, Ames (1989) demonstrated that dual inoculation with VAM fungi and actinomycetes could significantly increase the development of both the root and soil mycelia of the fungus, without adversely affecting plant (onion) growth. Reports on interactions of actinomycetes with rhizobia are few (see Barrion and Habte, 1988), and indicate that inhibitory effects by actinomycetes on rhizobia vary with the isolate-strain combinations investigated. In view of the ability of actinomycetes to control microbial populations (Trinick *et al.*, 1983), it is conceivable that proliferation of *Streptomyces* spp. on VAM hyphae may explain antagonistic effects observed between VAM colonization and nodulation (Bethlenfalvay *et al.*, 1985).

Summary

Seventy-five years ago, Jones (1924), working with pea plants, remarked that 'the root-inhabiting fungus is so abundant in plants that is it surprising to find that its presence is not common knowledge among botanists'. Today, the 'presence' has become known among plant scientists, but while we realize that a plant does not end at its root tips, an integrated view of the role of mycorrhizae in the tripartite legume association as a component of sustainable agro-ecosystems (Mosse, 1986; Sprent, 1986) is still lacking.

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