

THE MYCORRHIZAL PLANT-SOIL SYSTEM IN SUSTAINABLE AGRICULTURE

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EL SISTEMA SUELO-PLANTA MICORRIZICA EN LA AGRICULTURA SOSTENIBLE

SUMMARY

A sustainable farming system is biologically-based when its productive and supportive components, plant and soil, are in balance. This balance depends on the ability of soil and plant to support, in concert, a healthy and diverse native microbiota at the plant-soil interface, the rhizosphere. The soil microbiota enhances and mediates fluxes of nutrients from the inert soil matrix to the plant. The plant provides the energy to the biotic soil component whose activities, in turn, are crucial for the formation of physical structures and chemical balances within the soil matrix that permit and encourage the growth of roots. Among the multitude of soil organisms one type stands out because of its ability to form a bridge between plant and soil: mycorrhizal fungi. These fungi penetrate and colonize the cells of their host plant and the aggregates of their host soil, and form a living two-way transfer system for mineral nutrients from soil to plant and of carbon compounds from plant to soil. In the process they enhance plant growth and health, the proliferation of soil organisms, and the formation of soil structure without recourse to an application of chemicals. These fungi are therefore a key to biologically-based, sustainable farming.

RESUMEN

Un sistema sostenible de cultivo está basado en factores biológicos cuando sus componentes de producción y sostén, la planta y el suelo, están balanceados. Este balance depende de la capacidad del suelo y de la planta para mantener, en conjunto, una microbiota nativa diversa y saludable en la interfase planta-suelo: la rizósfera. La microbiota del suelo media y facilita los flujos de nutrimentos de la matriz inerte del suelo

a la planta. Las plantas proporcionan la energía al componente biótico del suelo cuyas actividades, por su parte, son cruciales para la formación de las estructuras físicas y los balances químicos en la matriz del suelo que permiten y favorecen el crecimiento de las raíces. Entre la multitud de organismos del suelo, una clase sobresale por su capacidad de formar un puente entre las plantas y el suelo: los hongos micorrízicos. Estos hongos penetran y colonizan las células de la planta hospedera y los agregados del suelo hospedero. Así, los hongos forman un sistema de transferencia vivo de dos vías, llevando nutrientes minerales del suelo a la planta y compuestos orgánicos de la planta al suelo. En este proceso, los hongos micorrízicos mejoran el crecimiento y la salud de las plantas, la proliferación de organismos del suelo, y la formación de la estructura del suelo sin necesidad de aplicar productos químicos. Estos hongos son por lo tanto de gran importancia para una agricultura sostenible basada en elementos biológicos.

WHAT ARE MYCORRHIZAE?

Vesicular-arbuscular mycorrhizal (VAM) fungi are symbionts of both root and soil. Structures of their root mycelia are in intimate contact with the cells of the root cortex, where they form finely-branched haustoria, or arbuscules. These arbuscules are the transfer sites for mineral nutrients from the fungus to the plant and for photo-assimilates from plant to fungus and ultimately to the soil. The soil mycelium is not limited to the rhizosphere, but ranges far out into the bulk soil (Camel *et al.*, 1991). The fine VAM hyphae penetrate the micropores of soil aggregates and are in intimate contact with the microbial colonies of both rhizosphere and bulk soil (Linderman, 1992). Obligate biotrophs, VAM fungi derive their requirement for reduced carbon from live roots. They share this carbon with the soil biota that may either utilize it in the form of exudates or by directly grazing on the hyphae. Thus, for the plant-soil biologist, the mycorrhiza, or fungus-root, is a symbiotic organism that connects the energy-converting plant shoot with the water and mineral supply of the soil, permitting this complex system to function as a continuum (Bethlenfalvay and Newton, 1991). In applied, agricultura terms, the mycorrhiza is a key to the yield-producing and soil-conserving functions of sustainable farming (Johnson and Pfleger, 1992; Miller and Jastrow, 1992b).

WHY ARE MYCORRHIZAE IMPORTANT?

Crop production in agricultural systems can be sustainable if the system is treated as an ecological unit (Allen, 1991; Sieverding, 1991). The unity of the ecological web of life is fragile, and agricultural practice is not possible without some disturbance. Mycorrhizal hyphae are still relatively little-known strands of this web; they do not yet figure prominently in the literature and discussions of agro-ecology. The reason for this is perhaps that work with soil microorganisms is more tedious and complex, and therefore more

specialized, than work with above-ground life forms (Linderman, 1988). Yet, soil organisms function in support of plant growth in many ways, and an impairment of any of those functions may result in a loss of sustained productivity. The functions range from chemical reactions mediated by microbial metabolism to the soil physics of the binding forces that help form clay micelles into aggregates (Hamblin, 1991; Tisdall, 1991). The conditions necessary to support these functions must be present, or restored if lost, to make farming not only an economic but also an ecological operation. Mycorrhizal fungi are central to the balance and coordination of plant and soil contributions to sustainability in agriculture.

MYCORRHIZAE IN AGRICULTURAL SYSTEMS

Unlike in natural ecosystems, where the limits of a community are defined by environmental stresses only, cultural stresses imposed by man contribute to the evolution and ultimate fate of an agro-ecosystem (Johnson and Pflieger, 1992; Sylvia and Williams, 1992). It is axiomatic that the severity of cultural stress should be inversely related to the sustainability of the system. Cultural stresses are manifold: they affect the plant, the soil, or both at the same time, and the effects of stresses applied to any part of the system are transmitted to other parts, often mediated by VAM fungi.

The stress most common in forage systems is clipping or grazing. When applied in moderation, the results may be beneficial. However, the loss of photosynthetic tissues affects not only the plant and its ability to regenerate shoot growth, but the availability of reduced carbon to the soil and its microbial communities (Bayne *et al.*, 1984). This process is mediated to a not yet fully explored extent by VAM fungi (Jakobsen and Rosendahl, 1990). Grazing pressure is always accompanied by soil compaction (Wallace, 1987). Since VAM fungi predominantly occupy soil layers at the surface, the impact on their soil mycelia is twofold: a physical disruption of the hyphal network and the crushing of the large and relatively thin-walled spores, in addition to carbon stress. Eventually the result is erosion, if an understanding of the system's stress limits does not lead to a timely introduction of proper management practices.

Soil disturbance is a stress universal in farming systems employing tillage. The effects of soil disturbance on plant nutrition are not well-known. Recently, a relationship was demonstrated between the disruption of VAM-fungal hyphae and phosphorus uptake by the host plant (Abbott and Robson, 1991; Evans and Miller, 1990). For optimum functioning, the plant apparently needs an intact hyphal network. Similar effects on plant nutrition are known to result from fallowing (Thompson, 1987). VAM fungi, as obligate biotrophs, cannot survive long without a host plant. When long fallow is practiced to conserve soil water, the population of VAM-fungal propagules may decrease in the absence of plants to a level where regeneration of the VAM soil mycelium is severely impaired. The result is phosphorus deficiency in the crop following the fallow. Thus, the

effects of two different practices, tillage and following, are similar and detrimental to the crop and are mediated by damage to the VAM endophytes. This may not be a problem when the farmer is able to supply fertilizers. However, in areas where agricultural chemicals are not available or affordable, the source of the problem must be recognized before it can be alleviated by such biological means as the cultivation and management of VAM fungi.

One solution to soil disturbance is a decrease in the intensity of tillage (Unger and Van Doren, 1982). Yet, in modern, conventional, chemical-based agriculture, no-till systems often require increased amounts of biocide applications to control weeds and pests (Cornish and Pratley, 1991; Phillips *et al.*, 1980). These biocides may control unwanted organisms, but in the process they are likely to affect nontarget organisms also (Vyas, 1988). Mycorrhizal fungi are such an unintended target. Since they are integral parts of their host plant (Gianinazzi *et al.*, 1982) and of the soil microbial population (Linderman, 1988) at the same time, they may be affected by biocides directly, or indirectly through effects on the host plant or on the host-soil biota (Trappe *et al.*, 1984). These complex interactions are important to sustainability, since biocide-induced retardation of VAM-hyphal growth, the inhibition of root colonization (Sattelmacher *et al.*, 1991), and a shift in species composition in the soil can be important for soil fertility and plant production (Dehn *et al.*, 1990).

Some chemical treatments are of interest to biologically-based farming because of their highly toxic effects on non-target organisms such as VAM fungi, while others actually enhance VAM colonization and sporulation (Vyas, 1988). Fungicides may also improve mycorrhiza formation by changing microbial competition in the soil (Schüepp and Bodmer, 1991) or by controlling plant pathogens (Afek *et al.*, 1991). VAM fungi may improve host-plant resistance to pesticide stress (Siqueira *et al.*, 1991). Utilization of biocides based on a knowledge of their effects on VAM fungi in addition to that on pathogens and pests is of practical significance in view of the potential of VAM fungi as biocontrol agents (Caron, 1989), and in view of their importance to the over-all health and development of the plant-soil system (Schönbeck, 1979).

PLANT AND SOIL INTERACTIONS

The rhizosphere, and the biological interactions that take place within it, is a concept dating to the beginning of this century (see Linderman, 1988). However, quantification of many functional aspects of these relationships has only recently begun (Curl and Truelove, 1986; Lynch, 1990). A large portion of the carbon input from the plant to the rhizosphere may be mediated by VAM fungi (Harris and Paul, 1987). The presence of mycorrhizal fungi can increase photosynthetic rates (Trent *et al.*, 1989), compensating for carbon losses to the endophytes. The flow of carbon from plant roots through the fungal and microbial biomass may be one of the key processes in terrestrial ecosystems (Jakobsen and Rosendahl, 1990; Van Veen *et al.*, 1989).

There are a number of positive feedbacks between plants and soil-microbe populations. Exudation from VAM roots and hyphae provides the energy that supports the diversity of soil microorganisms. Mycorrhizae are thought to be critical in the maintenance of soil aggregation (Miller and Jastrow, 1992a; Tisdall, 1991). Soil aggregation may be attributed to physical binding by roots and hyphae, gluing by microbially produced polysaccharides, or physical-chemical interactions between clay surfaces and partially decomposed organic matter (Strickland *et al.*, 1988; Tisdall and Oades, 1982). In many situations the loss of soil aggregation and structure reduces the capacity of soil to store nutrients and water (Rose, 1988). When soils are fallowed, or viring soils are cultivated, there is a loss of soil carbohydrates (Dalal and Henry, 1988), aggregates (Perry *et al.*, 1989), and of VAM-fungal populations (Thompson and Wildermuth, 1988). Thus, soil organisms may affect plant growth by improving soil structure (Miller and Jastrow, 1992b).

The implications of microbially-mediated changes in soil structure are important for sustainable agriculture (Reganold *et al.*, 1990). Soil structure affects infiltration and soil water dynamics, erosion potential (White, 1985) as well as nutrient cycling (Schimel, 1985). Thomas *et al.* (1986, 1992) demonstrated that VAM plants can increase the abundance of water-stable macroaggregates relative to non VAM plants. Thus, the influence of the fungus-root symbiosis on the soil must be part of the assessment of VAM effects on plant growth. Past emphasis has been on the plant, but interest in VAM effects may now shift to the soil. A fruitful area of research will be the evaluation of long-term effects of different plant and microbial communities on soil structure. If isolates of VAM fungi turn out to be effective in the transport of carbon to the soil without directly influencing plant nutrition (Bethlenfalvay and Newton, 1990; Miller and Jastrow, 1992b; Quintero *et al.*, 1992) the subject of "soil nutrition" will be interesting indeed.

PLANT TO PLANT INTERACTIONS

Nutrient transfer between the root zones of associated plants is influenced by VAM fungi, whose hyphae colonize and connect the roots of adjacent plants (Bethlenfalvay *et al.*, 1991). Past observations on nutrient fluxes between plants mediated by VAM fungi were summarized by Newman (1988). They suggested a concept of resource distribution in plant communities that is optimized by the movement of nutrients along concentration gradients between VAM donor and receiver plants (Read *et al.*, 1985). While the potential implications of this phenomenon for plant community structure are profound (Fitter, 1985), nutrient fluxes of sufficient magnitude to cause quantitatively important changes in plant growth or nutrition have not yet been unequivocally demonstrated (Hamel *et al.*, 1991; Hamel and Smith, 1991).

Nutrient fluxes between plants are of particular interest in legume-nonlegume associations (van Kessel *et al.*, 1985), because of the legume's role as a provider of

biologically fixed N to nonlegumes (Haynes, 1980). However, in simultaneous plantings, effects on grasses associated with legumes are mixed and can range from yield enhancement (Crookston and Hill, 1979) to yield decline (Hall, 1978). The effectiveness of N input into the intercrop system by legumes has been associated with the availability of phosphorus (Voss and Schrader, 1984), an effect recently confirmed by experiments involving mycorrhizae (Hamel and Smith, 1991). It remains to be demonstrated if VAM-mediated source-sink relationships determine the direction of nutrient fluxes between plants (Brown *et al.*, 1992). Effective utilization of VAM fungi in intercrops will require a determination of fungal compatibility with both host plants and an understanding of the timing of periods of peak sink demand by the associated plants.

CONCLUSIONS

Mycorrhizal fungi play a special role in the rhizosphere because they serve as the major link in the exchange of nutrients between plant and soil. In the process, VAM fungi enhance both plant nutrition and soil stability. Since soil stability is essential for the optimum growth of plants, we see a closed chain of cause-effect relationships in the function of mycorrhizal fungi in the plant-soil system: the fungi enhance plant growth through mineral uptake from the soil and by making the plants more resistant to stress; the larger plant that results has a greater carbon input into the soil which encourages the activity of the soil biota; the products of microbial metabolites improve soil structure; and better soil structure stimulates greater plant growth.

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