

## Interactions of Mycorrhizal Fungi with Soilborne Plant Pathogens and Other Organisms: An Introduction

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Roots support the growth of a complex of microorganisms that in concert can have a profound effect on the growth and survival of the plant. Up to 25% of the dry-matter production of the plant may be released into the soil in the form of root exudates and cell sloughage (1). Symbiotic mycorrhizal fungi, which are ubiquitous, obligate parasites of roots, require up to 10% of the carbon allocated to roots (6). Concomitant colonization and infection of roots by mycorrhizal fungi and by pathogens and other microorganisms inevitably lead to modification of each other's activities (7). These interactions have been of greatest importance to the pathologist when they result in weakened plants, but potentially beneficial interactions, if maintained or enhanced, could result in biological control of a pathogen.

The rhizosphere concept as it applies to roots is widely appreciated, but normally roots are mycorrhizal. It is tempting to speculate that the root cortex, which exudes nutrients (either passively or actively) and is vulnerable to pathogen invasion, has evolved to encourage colonization by mycorrhizal fungi and the establishment of a nutritionally effective symbiosis. Mycorrhizal colonization occurs after seed germination when the radicle is growing rapidly. At this time, the zone of elongation is most extensive, and the root has expended phosphorus (P) reserves from the seed. Root exudation is greatest in the zone of elongation, that portion of the root system where mycorrhizal colonization is initiated (12). Carbon losses from the root are sufficient to sustain the activities of the fungus (1), i.e., germination of spores, growth of hyphae to the root, penetration of the fungus between and into cortical cell spaces, and the development of external mycelia that take up phosphorus beyond the zone of nutrient depletion around the root. Before P sufficiency is attained, however, the root is at risk to pathogen invasion because cellular permeability is increased, due to phospholipid depletion in membranes, and root exudation is at its maximum (4, 10). As hyphal uptake of P occurs, root P content increases, membrane permeability is reduced, and more of the carbon is allocated to the mycorrhizal fungus in the root resulting in less exudation out of the root (4). Mycorrhizal-induced decreases in root exudation have been correlated with the reduction in soilborne disease (5). Thus, it is expected that mycorrhizae, through improvement of P nutrition, indirectly alter the activities of microorganisms that respond to quantitative changes in root metabolites in and around roots.

At this point, the rhizosphere becomes the mycorrhizosphere (7). No longer is the sphere of influence restricted to zones of soil around roots, but now occurs around hyphae extending from the root surface as well. The mycosphere exerts its own selective influence on microbial activities in the surrounding soil (7). This being the case, mycorrhizae may be a primary determinant in microbial management and biological control of soilborne pathogens. Even if the mycorrhizal fungus is not an antagonist per se, the successful exploitation of biological control requires that the biocontrol agent become established in the infection court, which is usually a mycorrhizal root. When there is a compatible interaction with the biocontrol agent in the rhizosphere, the mycorrhizal fungus in effect becomes an integral part of the biocontrol system.

The relationship between the host root and the mycorrhizal

fungus, an obligate symbiont, suggests that these fungi may very well interact directly with other root pathogens, such as nematodes, with similar trophic requirements. Plant-parasitic nematodes are antagonistic, obligate biotrophs, some of which feed on the cortical tissues of roots. The potential exists for competition with the mycorrhizal fungus for carbon and other nutrients, leading to reduction in infection or reproduction of the nematode. Nitrogen fixation by free-living and symbiotic bacteria may also be suppressed by the lack of carbon to support the high energy requirements of the fixation process. These types of interactions usually have been studied in P-deficient soils. Although mycorrhizal-mediated effects on host nutrition indirectly influence these interactions in most cases, it has not been possible to evaluate the direct interactions, such as competition for carbon, because of the improved P status of the mycorrhizal plant compared with the nonmycorrhizal plant. Fortunately, several recent studies have attempted to resolve this experimental shortcoming by comparing mycorrhizal and nonmycorrhizal plants of similar P status and size. We are now in a position to evaluate the direct interactions between mycorrhizal fungi and other organisms in roots and in the mycorrhizosphere.

The understanding of mycorrhizae as "an extreme form of parasitism" will undoubtedly shed light on the mechanisms underlying recognition and specificity, or the lack of it, between host and fungus. For example, there are no overt host defense responses when vesicular-arbuscular mycorrhizal (VAM) fungi penetrate roots. Furthermore, the concept of specificity has not been clearly demonstrated for any VAM fungus/host combination except those plant species that are found to be nonmycorrhizal in nature, such as members of the Cruciferae and Chenopodiaceae (9). The genetic and biochemical mechanisms that specify host and VAM fungus compatibility must be extremely general.

If there is a lack of host-fungus specificity and if root exudates are the driving force in the formation of the VAM symbiosis, then the activities of the fungus should be stimulated by root metabolites from a wide range of hosts. This appears to be the case (3). As mentioned already, improvement in P nutrition following VAM colonization of P-deficient roots results in decreased membrane permeability and reduction in root exudation (4). Although spread of the fungus slows after an initially rapid growth phase (2), colonization continues in spite of increased P nutrition. Reduced levels of cellular exudates may be adequate to sustain mycorrhizal activity because of the greatly enhanced surface contact between host cell membranes and the plasmalemma of fungal arbuscules. Thus, P control of membrane permeability to metabolites is a fundamental mechanism by which the extent of fungal growth in the root may be limited by the host.

In the case of ectomycorrhizal symbionts, basidiomycetes and ascomycetes, the penetration of the fungus between and into cortical cells appears to be limited by host production of phenolics (8) and, perhaps, phytoalexins. There also exists a high degree of specificity in these host/fungus relationships. Incompatible interactions proceed as in the compatible situation with spore germination, growth to the root and attachment, but there is limited penetration of root cortex. A similar incompatible response occurs in the interaction between VAM fungi and nonmycorrhizal species whose roots do not exude sufficient quantities of root metabolites to sustain infection (11) or whose roots contain toxins.

Basic understanding of mycorrhizal symbiosis may provide needed insights into the mechanisms of host root-pathogen specificity and the dynamics of rhizosphere processes. It is hoped that this symposium will lead to the recognition that mycorrhizae are a necessary consideration in future study of pathogenesis and microbial ecology of roots.

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