Mycorrhizae—Host Specificity and Recognition

Anne J. Anderson

Associate professor, Department of Biology, Utah State University, Logan, Utah 84322-4500.
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The mycorrhiza is a tissue in which metabolic harmony exists between two organisms, the fungus and the plant root. In general, mycorrhizal fungi are poor saprophytes or lack this ability entirely; they have developed a more secure food supply by cohabitation with the plant root. The plant, although capable of growth under sterile conditions, often has greater resistance to stress and higher productivity in the mycorrhizal state. These beneficial consequences of mycorrhizal formation enhance our desire to develop strategies to better use these fungi in plant management.

One strategy is to manipulate the genes that control the intricate growth of the fungus within the plant root. Comparison between mycorrhizal interactions and microbial pathogenesis suggests two roles for the genes that condition mycorrhizal formation. Certain genes must control the growth of the fungus to prevent pathogenesis. Other genes are involved in avoiding the resistance mechanisms of the root.

Mycorrhizal associations are not static interactions. Plant and fungal components are constantly in flux as hyphae colonize new host cells and extend into the rhizosphere. Because the fungus has evolved to cohabit with the plant tissue, molecular factors from the plant as well as from the fungus may act as keys to unlock the stages of the fungal life cycle. For example, the loss of ectomycorrhizal potential upon storage of fungi in culture (35) suggests that expression of genes controlling mycorrhizal formation may require certain plant factors. If recognition is defined here as an interaction between factors that leads to a result, the plant and fungal molecules that participate in the recognition events are crucial for mycorrhizal formation. Consequently, these recognition events result from the expression of genes that confer mycorrhizal potential. The complexity of the life cycle of the fungus within the plant indicates that compatibility cannot be the result of a single recognition event or a unique gene. Rather orchestration of the expression of many plant and fungal genes is involved. The diversity of type and effectiveness of mycorrhizae in the plant kingdom supports this concept.

What are the molecular keys for mycorrhizal compatibility? The recognition events likely to regulate gene expression and function probably involve extracellular components from plant and fungal cells. Many plant and fungal products have been implicated as key factors (28), including volatiles, hormones, lectins, and plant and fungal components with antibiotic potential. Some of these products and other components will be presented in this paper according to the zones in which molecular communication between plant and fungus can occur: the rhizosphere, the rhizoplane and the root epidermis, and cortex.

The rhizosphere. Components in the rhizosphere may promote spore germination. Enhanced germination in the presence of root exudates has been observed in Melin's classical studies for ectomycorrhizae (28) and more recently with vesicular-arbuscular mycorrhizal (VAM) fungi (26,29). Stimulation may involve more than just a provision of extra nutrients. Recent studies with *Rhizobia* and *Agrobacterium* have shown that certain phenolics actually prime the organism to become a plant colonizer (8,40). The phenolics induce the expression of genes that regulate other genes to produce factors essential for colonization. Phenolic concentration was critical because at high levels bacterial growth was inhibited. Although exudate compositions have been compared between mycorrhizal hosts and between mycorrhizal and nonhost species (47), emphasis has been placed on nutrient sources such as sugars, organic acids, and amino acids. Consequently, the role of phenolics in controlling gene expression in germinating spores of mycorrhizal fungi warrants investigation.

The rhizoplane. Structures at the rhizoplane may promote hyphae that have contacted the root to form a firmer attachment. Studies of other plant-microbe interactions indicate that recognition between lectins and specific carbohydrate structures is important in attachment. Plant wall structures with agglutinin activity have been proposed to aid attachment of zoospores of *Phytophthora* (37) and saprophytic (4) and avirulent pseudomonads (33). A search for lectinlike interactions between pine roots and surface components of an ectomycorrhizal fungus was unsuccessful (43). The lack of a recognition response may reflect on in vitro growth of the fungus used in these studies. Under these conditions, the hyphae would have lacked structures whose synthesis required induction by plant factors. The importance of the contact between the root surface and the hyphae is suggested by ultrastructural observations. Piché and Peterson (42) detected a fucose-rich polysaccharide associated with hyphae of an ectomycorrhizal fungus only when in contact with conifer roots. Defined fibrils were observed radiating from the hyphae of an ericoid mycorrhizal fungus in contact with plant roots (10). The absence of the fibrils on cultured hyphae suggests that the genes involved in expression of the fibrils could be activated by association with the host (10).

The epidermis and cortex. The mechanism, mechanical and/or enzymatic, of hyphal penetration into the epidermis and subsequently the cortex is unresolved. Ericoid and certain ectomycorrhizal fungi have been demonstrated to produce the plant cell wall-degrading enzymes pectinases and cellulases in culture (24). Repression of these enzymes by glucose is consistent with the need to restrain production in the mycorrhiza to prevent plant cell maceration. Attempts to demonstrate cellulase or pectin-degrading enzyme production from other ectomycorrhizae in culture (43) or in extracts from VAM ectonized tissue (Wood and Anderson, *unpublished*) have not been successful. Perhaps the assay conditions were inadequate or pectic and cellulytic enzymes may not be the sole keys for cell wall degradation. A role for the phenolic cross-linking of the plant cell wall protein extensin in generating the rigid wall structure has been demonstrated recently (15). A search for mechanisms that would destroy or prevent these types of cross-links may be profitable. The proteases produced by mycorrhizal fungi (6) could be involved in degradation of extensin. The alternative strategy, that polymerization of extensin is impeded by the fungus, supports a proposal discussed by Harley and Smith (28) in which fungal penetration inhibits plant cell wall formation.

Clearly, the invasion process is highly regulated, and we know nothing of the signals that determine the morphology of hyphal colonization in the cortical tissues. These signals result in the intricate web of branched hyphae of the Hartig net in the intercellular spaces of ectomycorrhizae. Intracellular growth occurs to produce the arbuscules in VA mycorrhizae and the coils of ericoid mycorrhizae. Ultrastructural studies by Bonafante-Fasolo and Grippiolo (12) have demonstrated that hyphal walls become less stratified during arbuscule development. Similarly, in older ectomycorrhizae the fungal walls and plant walls are less delineated than in the younger structures. Do these changes result from fungal cues or plant products? Perhaps the plant enzymes glucanase and chitinase, which are prevalent in the root, could be

involved in limited degradation of the hyphal walls.

Mechanisms to balance growth. What mechanisms are involved in balancing fungal growth in the mycorrhiza? Two possibilities will be discussed: the flow of carbon to the fungus and the role of plant defense mechanisms. Regulation of the flow of carbon to the fungus from the plant cell may limit the extent of fungal growth. This possibility is supported by the fact that glucose supplementation of roots caused hyphae of an ectomycorrhizal fungus to ramify extensively and produce plant cell necrosis (20). However, a certain level of nutrients from the root cells is essential for mycorrhizal formation. Leakage of nutrients from roots was demonstrated to be higher in plants that had greater potential to become mycorrhizal (47). Functional mycorrhizae even have been formed on a nonhost plant upon treatment with a herbicide that increased release of nutrients from the roots (46). Graham et al (27) proposed that carbon release increases with reduced phosphate nutrition in the plant because of altered plant plasmalemma structure. Mycorrhizal development then becomes self-limiting because improved phosphate availability donated by the hyphae to the plant would correct membrane permeability and restrict the carbon flux. These concepts are consistent with the dramatic seasonal flux of colonization by VA mycorrhiza of a cold desert grass (2). However, mycorrhizal fungi may play a more direct role in nutrient exchange. Wood and Anderson (*unpublished*) suggest that fungi may produce molecules targeted at enhancing nutrient exchange at the plant plasmalemma. If energy pumps are required for these processes, the plant plasmalemma ATPase may be one target. A role of the plant plasmalemma ATPase in nutrient exchange is supported from ultrastructural studies of endomycorrhizae. Enhanced plasmalemma ATPase activity was observed at the region of the matrix between the plant cell and the fungal hyphae (36). Auxin or other plant hormones produced by mycorrhizal fungi (28) may affect the plasmalemma ATPase. Auxin has been demonstrated to increase the proton efflux activity associated with the plant plasmamembrane ATPase (22). The altered pH caused by this interaction could regulate other metabolic events at the zones of contact between hypha and plant cells. One intriguing possibility is that the acidic pH would impair the polymerization of the extensin components of the plant cell wall (15). This suggestion may explain the observed lack of wall polymerization in the matrix between host plasmalemma and the arbuscule wall (19).

Induced plant defense mechanisms involving structural barriers, chemicals, and enzymes may also participate in restricting hyphal development. Mycorrhizal fungi have had to evolve schemes to avoid preformed host defenses. These schemes may include penetration of the epidermis through an appressorium formation or development of tolerance to phenolics in the barrier layer of woody roots (41). Enhanced phenolic accumulations have been reported for some mycorrhizal systems. Sylvia and Sinclair (49) demonstrated increased phenolic accumulations in the cortical cells of a compatible pine challenged with *Laccaria laccata* (Scop.:Fr.) Berk. & Br. in comparison with the unchallenged roots. The production of antifungal volatiles and phytoalexins is documented for orchid mycorrhizae (28). However, in general, induced phenolic responses are limited. Only a minor increase of phytoalexins was detected in VA mycorrhizal-soybean tissue (39). The activities of two key enzymes in phenolic metabolism (phenylalanine ammonia lyase and peroxidase) were similar in extracts from uncolonized and ectomycorrhizal roots (44). Piché et al (41) observed no elevated phenolic levels in their ectomycorrhizal system.

Presumably, the balanced and intricate growth pattern is essential for the nutrient exchanges that characterize the mycorrhiza (23). Use of radioactive tracers will increase our understanding of the nature of the exchanged components. Exchange of potassium has been examined by use of rhubidium (45). The demonstration by Ames of ^{15}N transfer from fungus to plant (3) has stimulated research into the enzymes that are involved in nitrogen utilization in mycorrhizal fungi (6), findings that will generate additional hypotheses.

Compatibility clearly demands essential recognition events between fungal and plant components that regulate development. These events are essential if the fungus is to demonstrate its full mycorrhizal potential and avoid incompatibility. The success of mycorrhizal fungi in colonizing nearly all of the plant kingdom reflects on the type of components involved in the recognition responses for mycorrhizal formation. As discussed by Trappe and Molina (50), these components must be essential for the survival of the fungus, the plant, or the mycorrhizal association.

Incompatibility. Absence or malfunction of the various recognition events essential for compatibility would result in incompatibility. Although incompatible interactions are in the minority, a situation that is the reverse of that of pathogenic fungi, incompatibility to mycorrhizal fungi does exist. Mycorrhizae are not formed with some plant species such as the Cruciferea and the Chenopodicea (28). Certain ectomycorrhizal and the ericoid mycorrhizal fungi display defined host specificities (28). For example, clover will not form a mycorrhiza with an ericoid fungus but will produce VA mycorrhizae. The enlightening studies of Molina et al (34,38) demonstrate that certain fungi form complete mycorrhizae only with restricted host species. This degree of specificity has not been demonstrated in VA mycorrhizae. Incompatibilities may not be so apparent with VA mycorrhizae because many studies have been conducted at a field level and concern the compatible interaction. In such studies, plants that lacked complete mycorrhizal formation would be ignored. However, there is documented variability in VA mycorrhizal efficiency between hosts (28). Aging impaired colonization to different degrees in clover and leeks (30). In the same study, one clover root was noted to impede colonization by a VAM fungus, perhaps because of a mutation in the plant (30). Studies of the mechanisms underlying such incompatible observations deserve greater attention. These studies would provide another approach to identify the plant genes that might be manipulated to exploit mycorrhizal formation.

Mechanisms controlling incompatibility may occur at each of the stages in the life cycle of the fungus, and plant factors may play key roles in controlling some of these events. The presence of plant toxins or lack of nutrients in the root exudate may limit germination. The absence of a recognition structure at the root surface may limit adhesion. However, results of several studies indicate that incompatibility occurred after germination, attachment, and limited penetration by the fungi. These studies include the interactions of conifers or eucalyptus with ectomycorrhizae (34,38), crucifers with VA mycorrhizae (25), and nonhost plants with ericoid mycorrhizae (11). Consequently, rhizosphere and rhizoplane events seem not to determine incompatibility in several systems.

Penetration at the epidermis or into cortical tissue can be regulated by chemical or structural barriers, which may be preformed or induced by the challenge. Lignification at the endodermis may account for the failure of hyphae to penetrate further than the cortex. Suberization of the epidermal cells is implicated as a preformed barrier for VA mycorrhizal fungi and may be related to the observed inhibition of mycorrhizal formation as roots age (30). Ultrastructural examination has shown the induction of barriers in the zone of penetration for VA mycorrhizae (9). In compatible interactions this collar of material around the infecting hyphae disappears and colonization proceeds. Failure of the collar to disperse could restrict growth. Induced production of phenolics may be significant. Molina and Trappe (38) and Malajczuk et al (34) report that phenolics accumulated at the site of the incompatible fungal challenge in conifers and eucalyptus. Bonfante-Fasolo (11) also observed necrosis of cortical cells of nonhost roots on contact with invading hyphae of an ericoid mycorrhizae. These responses resemble hypersensitivity, a frequent mechanism of resistance against fungal pathogens (17). Hypersensitivity may be induced in the plant cell by recognition of structures called elicitors (17). Characterized elicitors include fungal cell wall components, such as unsaturated lipids, glucans, and chitosan, and extracellular products including glycoproteins and polysaccharides (17). Pectin fragments, generated in plant cell walls by pectic enzymes, also have elicitor activity and can act

synergistically to promote the action of certain fungal elicitors (18). The question of whether mycorrhizal fungi produce elicitors and whether they are recognized by root tissues is one that is being addressed in my laboratory. Elicitors from ectomycorrhizal (14) and VA mycorrhizal fungi (Anderson and Wood, *unpublished*) have been detected on legume cotyledon tissue, but their role in the plant root has not yet been determined. The compatible plant root may not respond to mycorrhizal fungi because of masking of the elicitor structures on the hypha or lack of a functional recognition system. Additional fungal products, termed suppressors, have been proposed to impede elicitor detection in compatible plant pathogen systems (13). Thus, a balance between elicitors and suppressors may be involved in compatible mycorrhiza, whereas in certain incompatible interactions only the elicitors are effective.

Future directions. How can current technologies advance our understanding of mycorrhizal formation? Immunology offers the precision of recognition by monoclonal antibodies. The use of suppressants can permit selection of antibodies to unique features of mycorrhizal fungi. These procedures have demonstrated differences between races of the fungal pathogen *Phytophthora megasperma* (5) and to a limited degree between species of fungi causing wheat bunt (7). Partial differentiation between spores of VAM fungi has been achieved already using polyclonal antibodies (1,51). By raising antibodies to a specific structural component or an enzyme of a germinating fungus, the expression of this factor in a mycorrhiza could be detected using ELISA examination of mycorrhizal extracts. Ultramicroscopy using the antibody would determine the location of the factor in the mycorrhiza.

Nucleic acid hybridization techniques offer another method to determine whether a factor is being produced or is altered in mycorrhizal formation. Complementary DNA (cDNA) could be synthesized from the mRNA coding for selected factors and used as a probe. This technique has been used to determine the pattern of induction for enzymes of phenolic biosynthesis in plant defense responses against microbial pathogens (16). The probe could be coupled with ultramicroscopy and used for in situ detection of the mRNA. In situ hybridization has expanded the understanding of gene expression in many systems, especially *Drosophila* (31). Differential hybridization of mRNA from mycorrhizal and nonmycorrhizal tissues could indicate which classes of mRNA have altered synthesis in the mycorrhizal state. Related studies are examining differentiation in saprophytic fungi (52) as well as the plant genes that are involved in nitrogen fixation (21). Fortin and coworkers (32) are pioneering the use of 'new genetics' in the mycorrhizal field by the isolation of protoplasts from ectomycorrhizae and regeneration of mycorrhiza. Transfection of such protoplasts with selected pieces of DNA would permit the examination of exogenous genes in mycorrhizal development. For example, transfection may convert a nonmycorrhizal isolate of *L. laccata* to one with mycorrhizal potential. Once the genes are identified by transformation and other methods, the ability of plant components to regulate expression can be determined by using gene fusion with marker enzymes. This technique has been used to investigate the effect of plant phenolics in stimulating expression of genes in *Rhizobium meliloti* (40). The biochemical consequences of transformation to a mycorrhizal state could also be elucidated. Similar approaches are being employed in elegant studies to characterize avirulence genes in bacterial pathogens (48).

These examples illustrate how the molecular keys that condition the intricate synthesis of a mycorrhiza can be unlocked by our synthesis of traditional with developing technologies. We are at an exciting time when we can begin to explain at the molecular level how the fungus and plant root can coexist to form the beneficial mycorrhiza. This basic knowledge may permit genetic manipulations of plants and mycorrhizal fungi so that our agriculture can benefit.

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