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Mycorrhizal Fungi: Highways for Water and Nutrients in Arid Soils

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Mycorrhizal fungi are well known for increasing nutrient uptake but their effects on soil physical structure and water flow are less well understood. Here I explore what we know about the physical structure of mycorrhizal external mycelia and examine how that physical structure affects plant water uptake and reverse hydraulic lift in unsaturated soils. Mycorrhizal fungi are structured such that there are linear cytoplasmic units that can extend for a meter or more. Cell membranes may be only located in hyphal tips within the plant and externally several centimeters to meters distant from the plant root. Individual hyphae form a linear surface that goes across soil pores increasing the tortuosity factor (Γ) of the pathway for water flow, thereby increasing conductivity. But hyphae are small in diameter, providing only a small surface area for that transport. Little about the reverse flows (hydraulic redistribution from plant to fungus) is known other than that they occur and could play a critical role in sustaining hyphae through drought. The ultimate importance of mycorrhizae in plant–water relations depends on the drying patterns, the soil pore structure, and the number of hyphal connections extending from the root into the soil. New technologies are needed to adequately parameterize models of water horizontal flow patterns to: (i) observe and monitor the growth of roots and mycorrhizal fungi in situ; and (ii) describe the localized environment at high temporal and spatial resolution.

Abbreviations: AM, arbuscular mycorrhizae; EM, ectomycorrhizae.

There has been an increasing interest in the role of biological factors in affecting physical and chemical regulation of plant production, in both agricultural and wildland settings. In particular, the role of microbes in soil C and N dynamics has been studied extensively, but their role in passive processes, such as water movement, is less well understood. Fungi, in particular, may play a special role in soils. This derives from the fact that these organisms are not really microorganisms; they are macroorganisms packaged in microscopic units. Individual hyphae may only be 2 to 10 μm in diameter, but individuals can extend across many hectares. While they may weigh at most only a few percent of the soil mass, there can be several kilometers of total hyphae collectively in a single gram of soil (e.g., Bääth and Söderström, 1979). Because they are known to grow into soil pores down to 2 μm and even penetrate the rock matrix (e.g., Bornyasz et al., 2005), their importance should not be underestimated. Most of the research into fungal dynamics in ecosystems has concentrated on phylogenetics, degradation of organic materials, or mycorrhizal exchange of C and nutrients that do not move by mass flow. Much of the experimental research has either been undertaken in greenhouse pots, or has focused on the dynamics near the soil surface. Because of these foci, and the limited experimental analyses, we do not have a comprehensive view of mycorrhizal fungi and water relations in soils.

Mycorrhizal fungi represent a unique functional group in soil. Saprobic fungi use decaying material. While this is a large fraction of the soil organic matter, much of the C is decayed during a period of at least a year (Gaudinski et al., 2000) and any other resources transferred only indirectly. Like pathogens, mycorrhizal fungi acquire C directly from the plant. But, pathogens generally use only a small fraction of the net primary production. Mycorrhizal fungi generally acquire between 10 and 30% of the plant's net C fixation as an average (e.g., Finlay and Söderström, 1992; Allen et al., 2003). In most ecosystems, this allocation dramatically exceeds loss due to pathogens, but as plant growth generally increases with vs. without mycorrhizae, this loss is generally ignored. Microbial turnover is generally modeled on the order of hours to days. Mycorrhizal fungal tissue has a wide variation in lifespan. Sporocarp tissue $\delta^{14}C$ analyses suggest that most of the extramatrical fungal tissue is recently fixed C (within a year), although individual root tip C can exceed 3 yr (Treseder et al., 2004). The production and turnover of the C forming individual mycorrhizal hyphae is within a few days (Staddon et al., 2003). Our most recent estimates using daily measurements of hyphal and rhizomorph lifespans suggest that individual coarse hyphae live for an average of 12 d, and Treseder

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et al. (2005) found that rhizomorphs lived for an average of 11 mo. But individual rhizomorphs have been observed surviving for up to 7 yr (unpublished observations, 2005).

There are several recognized types of mycorrhizae, ranging from highly specialized orchid mycorrhizae to ericoid mycorrhizae that have little external hyphae, to the poorly understood dark-septate types. In this discussion, I will focus on arbuscular mycorrhizae (AM) and ectomycorrhizae (EM). These types have broad distributions and are the best studied of the mycorrhizal types. The AM are formed between most vascular plants and fungi in the *Glomeromycota*. This symbiosis is phylogenetically the basic form for terrestrial plants—all land plants evolved from those forming AM (e.g., Malloch et al., 1980; Allen, 1991). The EM are more complex in that this mycorrhiza form has evolved independently many times in both plants and fungi. For this reason, it is often more difficult to generalize about structure–function relationships in this symbiosis.

Mycorrhizal fungi are best known for their ability to take up and transport nutrients to the host plant in exchange for the plant's C. But experimental evidence tends to focus on systems in mesic regions, in irrigated agriculture or in greenhouse conditions. Thus, these studies have tended to focus on conditions near soil saturation to the point of "permanent wilting," or approximately −1.5MPa, when soil pores remain relatively filled with water. In many of these cases, mycorrhizae alter plant–water relations, but these are largely attributed to indirect effects on plant nutrition (e.g., Safir et al., 1972), osmotic adjustment (Allen and Boosalis, 1983), or phytohormone regulation (Allen et al., 1982). These factors were recently reviewed (Augé, 2001).

The potential role of the hyphae themselves as a regulator of plant water uptake remains a controversial issue, however. Because of their individually small size, and because they are "microorganisms," one view is that the hyphae themselves cannot directly alter water flows. Further, creating unambiguous experimental conditions that test for the role of hyphae in soil water dynamics remains challenging. The only constant remaining is that water and nutrient movement along hyphae in soil has remained a mechanism that, if correct, has enormous impacts on water and nutrient management. This is especially relevant today as water conservation in irrigated agriculture becomes of greater concern and ever-greater demands are placed on dryland agriculture in areas with rapidly growing populations. Thus it remains critical to understand how something as seemingly small as a fungus could possibly become a useful tool in managing soil water.

Microscopic and Macroscopic Structure of Hyphae

While fungi are often measured as part of the soil microbial mass, their structure is so radically different from prokaryotes that lumping them together provides a misrepresentation of the functional processes they undertake. Fungi are eukaryotes whose individual cells are linearly organized to form a hypha, which merges into a complex network known as a mycelium. An individual fungal cell consists of a cytoplasm tube bounded by a membrane, surrounded by one or more wall layers (see Allen, 2006). Two particularly relevant features emerge. First, the cytoplasm has few to no membranes separating the hyphal tips. Even in those fungi with septa, the walls have pores between "cells." Even structures as large as nuclei move from one cell to another through these pores. Individual molecules such as water can diffuse readily from one point to another along gradients. Arbuscular mycorrhizae rarely have cross walls (and these are adventitious, probably forming in response to wounding or other perturbation). Second, the newly produced hyphal tips have fewer wall layers, and they tend to be hydrophilic. Water is taken up or transpired at the tips and translocated within the hypha. The direction depends on the water potential gradient. This transport is regulated by the membrane, allowing hydrostatic pressures to accumulate, one of the driving mechanisms for growth. But as an individual hypha ages, it accumulates hydrophobic layers, meaning that water tends not to be exchanged with the soil through this portion (Unestam, 1991).

A mycorrhizal hypha has two groups of hyphal tips of particular relevance. The first set are located within the plant. In an EM, these hyphal tips are found between the root cortical cells, in a hyphal matrix known as the *hartig net*. In an AM, these hyphal tips penetrate the wall but not the plasmalemma of cortical cells and form intracellular coils or arbuscules. These tips are very dynamic. Arbuscules only live a few days. Although we do not know the age of individual hyphae in a hartig net, I would postulate that they are quite dynamic. The remaining external hyphae extend from an infection point into the soil matrix and constitute the largest biomass fraction of the fungus, but that portion is crucial to our discussion here. What this means is that water can be taken up by a tip in the soil, and transferred through either the cytoplasm or through the inner wall layers, from an individual soil pore, along a hypha, to a cortical cell within a layer or two of the endodermis, without encountering a membrane except at the soil entrance and root exit. The water within a hypha is protected from the external soil environment by hydrophobic walls except at those tips.

That external hydrophobic structure also plays an important role in water flow. The surface of the hypha acts as a solid surface. In this case, the surface tension causes an attraction of water to the hyphal surface. Water can be observed flowing along the surface of mycorrhizal hyphae in unsaturated soil between glass plates (e.g., Allen, 1996). As soil dries out, the thickness of the water layer decreases, forming a narrow group of "bundles" surrounding individual hyphae. The importance of this layer will be discussed in greater detail below.

Fungal hyphae have an additional architectural feature that also makes mycorrhizae important to water dynamics. Individual hyphae will wrap around each other, forming a space between linear, hydrophobic surfaces. More primitive fungi, such as AM hyphae, can form wrapping "networks" of two to five hyphae extending a few centimeters into the soil (Allen, 2006). In some complex basidiomycetes, these fungi can form highly structured "chords" that have vessel elements that are known to rapidly transport water and nutrients (Duddridge et al., 1980). These linear groups of hyphae increase the thickness of water "bundles" by protecting even the external hyphae from the outside drying soil pores.

Fungal hyphal length in soil can constitute up to 1 km/cm^3 of soil and AM fungal hyphae can exceed 10^8 m/m^3 (e.g., Miller et al., 1995). In AM systems, there are two types of mycelial networks that are of interest. The first is the "runner" or "arterial"

hyphae that extend from an infection point into the soil matrix looking for nutrient resources or new root tips available for infection. These hyphae tend to be large (often 10 μm in diameter or larger), with relatively infrequent branching. The second are the absorbing hyphae, a dichotomously branching network, each branch of which gets narrower. Friese and Allen (1991) found that each branch extended about 5 mm, with up to eight branching orders. They reported a branching absorbing network for each infection point. Absorbing networks thus have a distinct fan-shaped architecture starting with a single large hypha, branching into two smaller hyphae, branching into four smaller hyphae, and so forth, to an eight-order branching unit, with 128 tips, each about 2 μm in diameter (Friese and Allen, 1991; Allen et al., 2003). The absorbing unit extends about 6 cm into the soil from a root. Bago et al. (1998) described another architectural form in that an absorbing network could form from arterial hyphae, dramatically extending the potential network well beyond that reported by Friese and Allen (1991). Together, these mycelia provide a network of well over 100 cm of hypha per infection unit, extending several centimeters into the soil from the root surface. Commonly, we find approximately one infection unit per millimeter of root length, a value Fitter (1991) reported as optimal for uptake of P from soil. Importantly, these networks extend from the root system into the bulk soil, well beyond the zone occupied by the roots and root hairs (Fig. 1A).

The EM have a wide variation in structures, ranging from fungi like *Cenococcum* that form intensive, hairy networks around individual roots, to those like *Pisolithus* sp. with extended rhizomorphs that extend several meters into the surrounding soil. An EM infection is usually a single root tip or set of root tips that is encased within a fungal mantle. Individual hyphae or organized mycelial networks, known as chords, extend from those individual infections into the surrounding soil (Fig. 1B). Sporocarps of EM fungi have been found up to 20 m from a host tree (Allen, 1991). Just as importantly, mycelia form large networks that have the capacity to connect individual plants. It remains virtually impossible to follow an individual mycelium through soil, but field assessments show the presence of a taxon across a large area that often can result from an individual (Fig. 2). Transport studies have shown that, in some cases, resources such as C or N can be transported between individual plants through these "common mycorrhizal networks" (e.g., He et al., 2006).

Structure of Hyphae and Soil Structure: Bridging the Gaps

The mycorrhizal mycelium network comprises either a dichotomously branching (AM) or a net-forming architecture extending from an infection into the soil matrix (Allen, 1991). Because mycorrhizal fungal hyphae extend from the plant into the surrounding soil, and extend up to several centimeters, they bridge gaps across soil pores. These hyphal bridges can occur across macropores when soil particles or rocks predominate, or across smaller pores in finer textured soils. On Mount St. Helens, plants had to establish on pumice that had virtually no water-holding capacity; water drained through the pumice rapidly, leaving the plants in a highly unsaturated substrate. The first colonizing plants were *Lupinus lepidus* Douglas ex Lindl. These lupine plants tend to have little growth response to

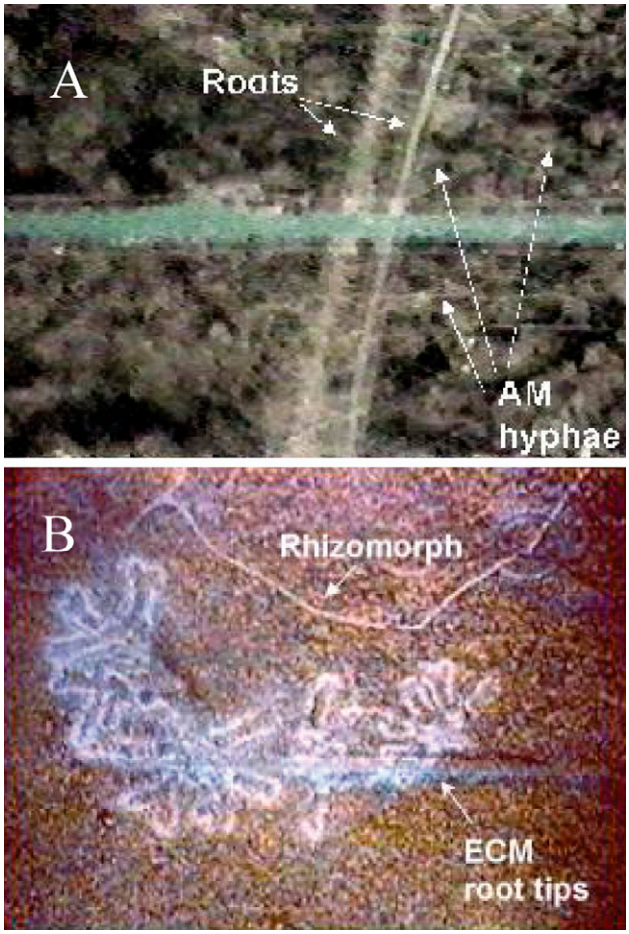

FIG. 1. Mycorrhizae in situ: (A) arterial arbuscular mycorrhizae (AM) hyphae extending from a root of *Artemisia californica* beyond the root hairs into the surrounding soil matrix, and (B) an EM infection consisting of several root tips encased in a fungal mantle, with a rhizomorph extending from those tips into the surrounding soil. Both images were acquired using a Bartz Technology Corp. minirhizotron, Model BTC-100X.

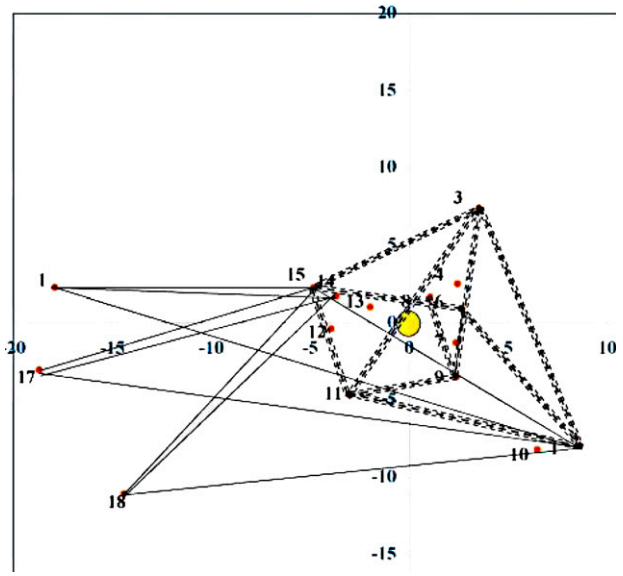

FIG. 2. The expanse of a single fungal taxa connecting a mature oak located at the 0,0 point with seedlings planted at various distances (in meters) surrounding the mature tree. Shown are two taxa, *Thelephora terrestris* (wide dashed lines) and *Amanita* sp. (narrow solid lines) based on distribution of restriction fragment length polymorphism analyses of seedling root tips (Allen and Lindahl, unpublished data, 2003).

mycorrhizae in the greenhouse (Titus and del Moral, 1998) but they do form mycorrhizal associations. In the pumice material, Allen et al. (1992) found that water conductivity increased in mycorrhizal compared with nonmycorrhizal lupines in unsaturated soils. In later examination, I observed that individual pieces of pumice would hold water, but that the pathway through which water would have to flow to reach plant roots can be a long distance between particles. The AM hyphae clearly bridged those gaps (Fig. 3).

The outcome of this response is a reduction in tortuousity as the soil moisture drops below −1.5MPa. The importance of these hyphae is that they reduce the capillary length of the water pathway compared with the column length. Jury et al. (1991) describe one means of understanding hydraulic conductivity, expressed as a function of the tortuousity (Γ) and the summation of numerous capillary "bundles" of water, where

$$K(\theta) = 1.14 \times 10^{-6} \Gamma \sum_{J=L+1}^{M} h_J^{-2}$$

where $K(\theta)$ is conductivity at a known water content, and h is the matric head as the soil water decreases, J is a single capillary size class, with L capillary tubes, and M is the number of capillary size classes. From a suite of studies, Γ has been modeled as

$$\Gamma = L/L_c$$

where L is the column length and L_c is the capillary length. In this case, the role of the hypha is to reduce L_c by serving as a surface for capillary bundles stretching across solid surfaces from a saturated pore to the root. The contrasting point, however, is that the number of "bundles" also declines because the viscous flow along a hypha is very small due to the small size of an individual hypha.

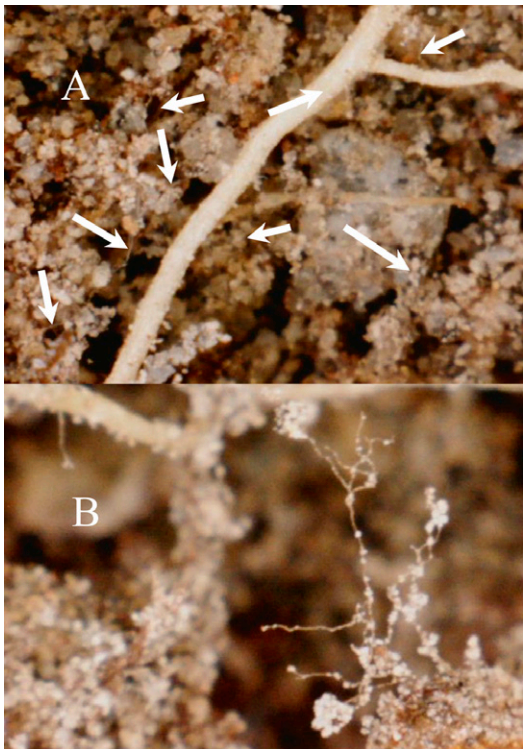

FIG. 3. (A) An arbuscular mycorrhizae (AM) hypha bridging gaps between pumice particles on Mount St. Helens. (B) After teasing apart pumice pieces, the AM hyphae connecting pumice particles and the roots can be clearly seen. Images were taken using a Scalar Proscope USB digital microscope at 100×.

The potential for hyphae to reduce Γ can be visualized in microscopic images taken using the minirhizotron. We developed a method that identifies edges. Edges represent a two-dimensional representation of a three-dimensional structure. From minirhizotron images, we can visualize clear linear structures of root and rhizomorph edges that show that L_c can approach L (Fig. 4).

Support for this role can be found in two recent studies. Augé et al. (2004) found that the presence of mycorrhizal fungal hyphae could contribute to soil hydraulic conductivity even in plants not forming mycorrhizae. Querejeta et al. (2003b, 2007) found that hydraulically lifted water was translocated from the plant into the soil via the hyphae and emerged from the hyphal tips. That water did not flow through the soil matrix.

An additional location where a reduction in Γ could play a critical role is in accessing water where roots cannot grow. Hubbert et al. (2001) demonstrated that weathered granite serves as a critical source of water in seasonal drought environments, such as southern California. While roots penetrate fault lines, they cannot penetrate the rocky matrix where much of the water is stored (Bornyasz et al., 2005). Recent isotopic analysis has shown that this matrix is a measurable source of water for coast live oak (*Quercus agrifolia* Née; see Allen, 2006). The Γ value for flow in this matrix has not yet been calculated, but the distances of unsaturated flow along the granite pore sides must be rather high. The EM fungal hyphae of conifers and ericaceous plants penetrate weathered granite (Egerton-Warburton et al., 2003) and feldspar (Hoffland et al., 2003). Both EM and AM fungal hyphae also penetrate granite (Bornyasz et al., 2005) and limestone (Estrada-Medina and Allen, 2005, unpublished data). Analyses show few C or nutrient resources other than water available in the rock matrix. This provides indirect evidence that mycorrhizal fungi may also play a critical role in tapping what are relatively unavailable plant water sources under drought conditions.

Limitations to the Importance of Hyphal Transport: Not Too Wet, Not Too Dry, Not Too Large, Not Too Small

Greenhouse studies abound that show or fail to show mycorrhizal enhancement of plant–water relations (Augé, 2001). Much of the problem lies, in part, with the particular conditions in which the different experiments were undertaken. Under saturated soils, it is unlikely that mycorrhizal hyphae would directly increase plant water transport because the surface area for transport via the hyphae remains small in comparison with the total root surface area. Although mycorrhizae can enhance water throughput under these conditions, the mechanism is likely to be indirect.

In a field study on mycorrhizae and water relations, Allen and Allen (1986) reported that mycorrhizae enhanced the plant water throughflow at the critical point when leaf water potential (ψ_l) ranged from −2 to −3.5 MPa, and soil water potential (ψ_s) in the rooting zone was between −1.5 and −2 MPa. Subsequent work by Querejeta et al. (2003a, 2006) demonstrated that AM could enhance water throughput and, based on $\delta^{18}O$ ratios,

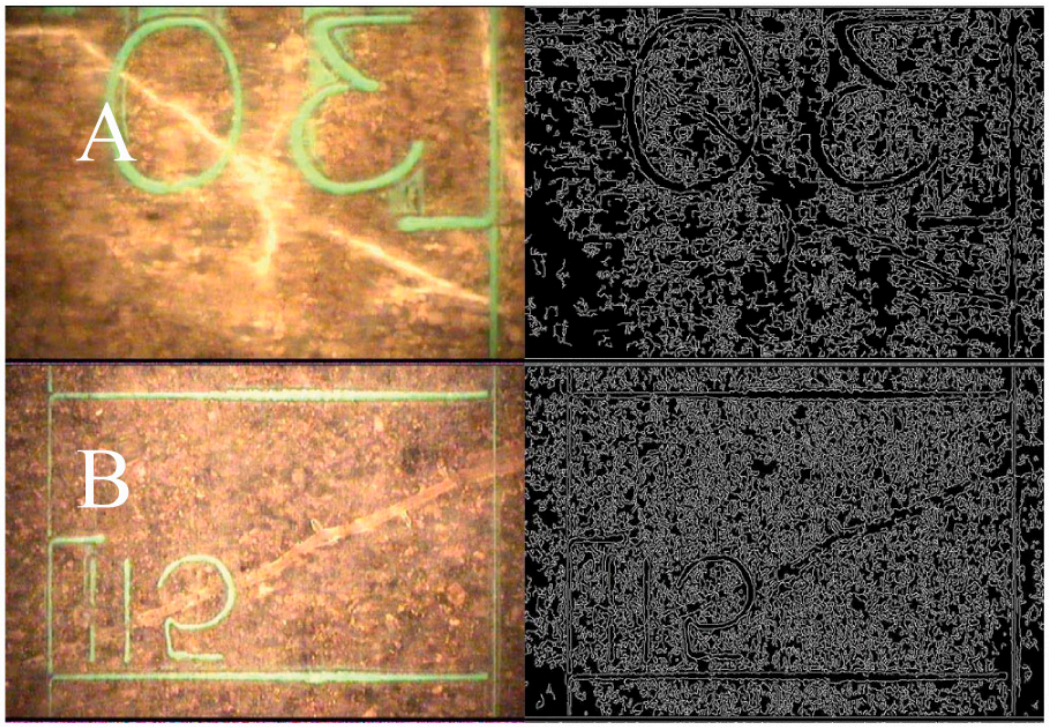

FIG. 4. Changing the tortuosity factor Γ by crossing gaps of soil pores. Roots, rhizomorphs, and individual hyphae can reduce the Γ by reducing the capillary length (L_c) compared with the column length (L), by providing linear units crossing soil pores. The two examples show these linear units. The left images are minirhizotron photos and the right images are from a program that identifies edges, showing the structure of the edges created by the roots and rhizomorphs. (A) shows a root stretching across a minirhizotron frame and (B) shows a rhizomorph. In both cases, the soil pores are outlined in small spherical objects, whereas the roots and fungal hyphae are linear units.

it appears that much of this difference could be related to the external hyphal matrix.

Clearly, if we are to understand the conditions when fungi do or do not alter water relations, we must return to understanding the pathways of water flow in soil and tease apart when these organisms do and do not affect water dynamics. One of the first issues may well be the soil pore size in comparison to the size of roots and root hairs. Macropores are larger than 80 μm, and mesopores go down to 30 μm. Many fine roots can penetrate macropores, and most root hairs penetrate mesopores. When macropores and mesopores are water filled, water transport along mycorrhizal hyphae is likely to be negligible. Fine root hairs, such as grasses, even penetrate the larger micropores. But mycorrhizal fungal hyphal tips are as small as 2 μm, capable of growing into the largest of the ultramicropores. At $\psi_s < -1.5$MPa, most of the mesopores and larger micropores containing roots no longer contain water. As long as there are water-filled micropores, the water flux is a function of the hydraulic conductivity and the change in water potential. As the soil dries, the water column retreats into micropores that are not accessible to roots or root hairs. In micropores, the distance to the meniscus approaches infinity without a mycorrhiza. But with up to 128 (or more) hyphal tips, each as small as 2 μm in diameter, for each millimeter of root length probing soil pores, micropores, or larger ultramicropores, some water could be accessed.

Examining the relationship between the hyphal diameters and the numbers of hyphae necessary to influence plant–water relations is a topic for further detailed modeling activity, but remains an intriguing area for work. In the models of water conductivity in unsaturated conditions, while the hyphae can raise Γ, they support far fewer "bundles"—viscous layers—than a much larger root or root hair. Is this adequate to make a difference to plants? Allen (1982) calculated that to account for the difference in mycorrhizal water transport, the hyphae at the root interface needed to transport up to 100nL/h. This value is a very high rate of transport, although in this system, the transpirational demand was exceedingly high. Cowan et al. (1972) reported flows of 131 nL/h in *Phycomyces blakesleanus*; Cooke and Whipps (1993) and Eamus and Jennings (1986) reported cytoplasmic flows of 20nL/h in more mesic conditions. These measurements included only cytoplasmic flow, not the wicking externally along the hypha, which is perhaps the largest fraction. Clearly, there is a lot remaining to be studied both through modeling and experimental efforts before we will understand the dynamics of water flux in individual hyphae.

Bidirectional Flows in Mycorrhizal Hyphae

Recent evidence also suggests that mycorrhizal hyphae may be serving as a critical bridge in the opposite direction. Hydraulic lift, or, more accurately, hydraulic redistribution, may both play a critical role in plant persistence during drought, and affect plant–plant interactions (Caldwell et al., 1998; Dawson, 1993). This process does not appear to occur under conditions of high soil moisture in the surface (e.g., Brooks et al., 2006), but only as ψ_s declines below −1MPa. We recently reported that hydraulically lifted water could be transferred to both EM and AM fungi. In the lab, water could move several centimeters into an adjacent chamber into which mycorrhizal hyphae, but not roots, could grow because of restrictions by mesh filters and air gaps (Querejeta et al., 2003b).

This process is relatively straightforward, but structurally complex. Under conditions with dry surface soils but deep water, plants such as oak take up the deeper water. This water is then distributed throughout the root profile, sustaining mycorrhizal fungi through the dry season. Where oak cannot reach deep water, or in shallow-rooted systems, hyphae decline during the dry season (Querejeta et al., 2007). During the daylight, normal transpiration occurs. At night, however, the driving ψ gradient is from the stem into the fine roots in the surface soils as the stomata are closed. Using a series of dyes and isotope analyses, we found that water moved through the endodermis,

into the hartig net (in EM) or intercellular hyphae (in AM), and flowed out the hyphae. The labeled water continued internally through the hydrophobic portion of the rhizomorph or individual hypha to the hydrophilic tips, where it was exuded into the soil. The water exuded into the soil could then be taken up the next morning by hyphae attached to the original tree, or even to a nearby one (unpublished data, 2005). Importantly, we failed to find evidence of the hydraulically lifted water in the soil adjacent to the root itself. Instead, the dyes were distributed along mycorrhizal hyphae, through the meshes and air gap, and into the hyphal-only chamber. We did observe the dyes in organic matter exuding through the hydrophilic hyphal tip (Querejeta et al., 2003b).

We recently began studies to measure and observe short-term mycorrhizal dynamics in the field. Surprisingly, there was a lot of EM fungal growth even when ψ_s was lower than −4 MPa, the limit of our soil moisture sensors (Fig. 5). An AM fungal hyphal network developed from an AM root tip during the course of 2 wk during July, when soil moisture was below 1%, or −5MPa. One hypothesis is that this water comes from hydraulically redistributed sources from deep in the profile (Querejeta et al., 2007).

Conclusions

Integrating Time and Spatial Scales: New Technologies

Observations of hyphae penetrating weathered rock, existing deep in the soil profile, and growing in soils at very low water indicate that we still have much to learn about the complex water movement patterns in soils. This is particularly true in complex soils that exist in forests that undergo seasonal drought and in irrigated perennial orchards. If we are to manage water carefully, we need to understand the roles of all factors that regulate water movement patterns.

Part of the difficulty is that soil scientists have focused work on the abiotic properties of water movement in annual, tilled croplands with intensive fertilization, where mycorrhizal fungi have been lost or dramatically reduced. Under annual tillage, the species of fungi that do persist tend to have a small hyphal network (e.g., Allen and Boosalis, 1983). This contrasts with perennial systems with fungi forming an extended network that can take several years to develop (Weinbaum et al., 1996). Soil microbiologists, on the other hand, have tended to view soil fungi as part of the "microbial biomass," whose larger functions are primarily C and nutrient transformations. Under this focus, there are a large number of studies measuring microbial biomass using indirect techniques (serial infrared, chloroform fumigation, plate counts), but largely without considering the effects on the physical structure of the soil.

Another difficulty is that point measurements are taken (in space and in time) or models that are based on experiments from the laboratory are extrapolated to the field. These are necessary limitations to understanding water dynamics. But teasing apart dynamics using point measurements and extrapolating complex field dynamics from simplified laboratory experiments remain difficult. There is simply no substitute for being able to observe and measure soil dynamics in real time in the field.

Recent technological developments offer hope to move in these directions. Automated soil moisture and temperature monitoring capabilities have been available for some time, but still are not widely used. Further, these do not monitor horizontal flow, although vertical flows are often measured. To assess horizontal flows, especially for studying the roles of fungal hyphae, new horizontal-based sensors of fluxes are desperately needed. New soil CO_2 sensors are providing interesting insights into respiration of roots and microbes in situ, rather than simply making difference calculations (Tang et al., 2003; Turcu et al., 2005). Development of probes that monitor nutrient changes are available for aquatic systems, but are still needed for unsaturated soils.

Minirhizotrons have been used extensively for monitoring root dynamics; however, individual images require an observer to differentiate roots from soil particles. The resolution of most minirhizotron images is not adequate to differentiate soil fungal hyphae, although rhizomorph dynamics can be readily studied (Treseder et al., 2005). The developments in the newer USB-port microscopes hold promise for developing in situ microscopes capable of observing soil phenomena during short-term intervals.

Together, these monitoring tools should help parameterize soil water models, but the scales must be made smaller in space and shorter in time. It is only with higher resolution information that we can tease out the surprising roles of fungi, with properties of both macroorganisms and microorganisms.

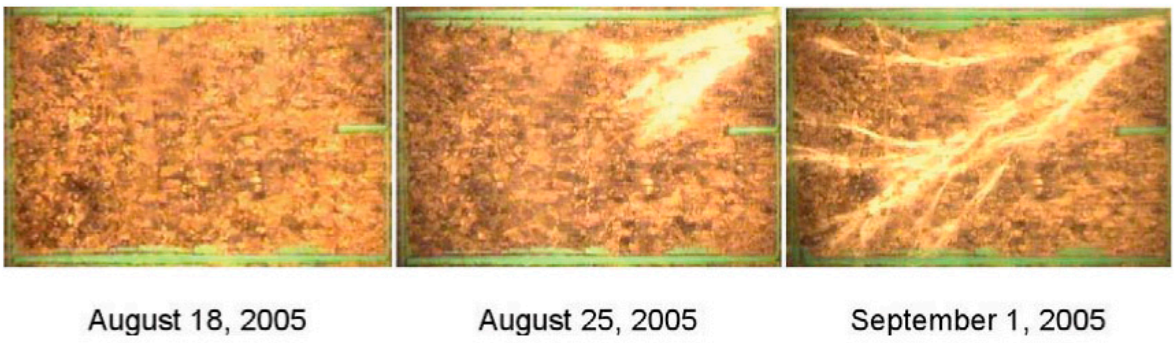

FIG. 5. The growth of ectomycorrhizal rhizomorphs in the surface soil at the James Reserve, in the mixed conifer forest on Mount San Jacinto. The nearest tree is a ponderosa pine, whose roots probably extend to the groundwater, several meters below the soil surface. These images were taken during the dry season; surface soil moisture sensors (where these images were taken) stopped recording in July, when the soil moisture declined below the detectable levels. We estimated that the soil water potential was between −4 and −5 MPa, below what should be necessary for hyphal growth unless there is another source at the distal end of the rhizomorph. We postulate that this source is hydraulically lifted water. Similar phenomena were observed for individual hyphal networks of arbuscular mycorrhizae fungi (Allen and Stozle, unpublished observations, 2005).

Acknowledgments

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