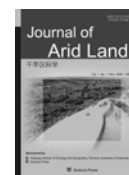# Linking water and nutrients through the vadose zone: a fungal interface between the soil and plant systems

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Abstract: Plant water availability, use, and management have largely focused on physical processes of infiltration and the role of roots in uptake and transpiration. However, roots and mycorrhizal fungi redistribute water in complex patterns. Here I describe some of our observations and experiments showing that mycorrhizal fungi play key roles in moving water for both transpiration and to facilitate nutrient acquisition under dry conditions. Mycorrhizal fungal hyphae grow from both surface and deep roots even into bedrock to help extract water under dry conditions. In both deep and surface roots, mycorrhizal fungi acquire water from pores too small for roots and root hairs to access, and at distances from roots and root hairs. Mycorrhizal fungi are also able to utilize hydraulic-lifted water from plants to obtain nutrients in extremely dry surface soils. The importance of these root symbionts in water and nutrient dynamics, and as integrators of surface and deeper water dynamics need further investigation.

Keywords: mycorrhiza; vadose zone; hydraulic redistribution; drought

Predicting water use by irrigated crops in mesic lands has become relatively accurate, facilitating manipulation of water application and for predicting crop growth and production. However, these models are largely based on the relatively even distribution of soil structural elements through the root zone, coupled with an understanding in the vertical spatial distribution of water inputs. Even then, however, water movement within the soil profile is chaotic, resulting in complex patterns of water movement under unsaturated conditions. Much of the research on water movement and use has been undertaken as a physical process, but here I discuss the role of mycorrhizal fungi in redistributing soil moisture for plant use and for plant re-allocation to mycorrhizal fungi to acquire surface nutrients.

Water and nutrients are tightly coupled in regulating ecosystem processes including productivity and decomposition. However, in arid land soils, water and nutrients are spatially segregated. Most of the nutrients are applied (as fertilizers) or continually cycled in the upper soil layers and the highest nutrient availability is generally in a thin organic layer between the litter and the mineral soils, and in the upper mineral soil. In mesic climates, or following large precipitation events, plants can shift to using this deep water (Brunel et al., 1995; Li et al., 2007). However, in arid lands, as soils dry out, available water drops deeper into the soil, even into perched water pockets or the rock layers, creating a dry zone with complex patterns of water distribution and movement. Following irrigation or precipitation, particularly summer thundershowers, water may infiltrate to just below the upper soil surface, creating a dry layer between the surface moist layer and the bedrock, or groundwater. In predominantly winter precipitation regimes, summer precipitation events can provide some moisture for processes such as decomposition, but has been often assumed to be of little value to the plant (Cui and Caldwell, 1997). That may not be an accurate assumption. In warmer regions with summer precipitation, repeated filling and drying of surface soils, then long-term drying of the soils through the dry season is common.

Arid ecosystems are infinitely more difficult to model and manage than mesic-region croplands

because the spatial and temporal variability resulting from complex soil structural elements, water inputs, plant water extraction, and evaporation can be quite different among adjacent cm^2 of soil and from moment to moment. However, important information on water use by wildland plants should improve management of water in irrigated fields, especially in perennial crops such as vineyards and orchards. In furrow irrigation, plant roots occupy the ridges between the trenches, with water penetrating soil down below the furrows and horizontally into the ridges. More efficient irrigation systems, such as drip irrigation, also result in complex spatial patterns of water input.

In wildlands, rain can be deflected from the canopy surfaces, or preferentially directed such that it runs down tree trunks creating complex infiltration patterns. That water then runs across the soil surface in intricate patterns, again creating a complex input pattern of soil water (Hastings *et al.*, 2005). Snow tends to accumulate between tree canopies, being intercepted by those canopies; or with melt, running down trunks or drop in small patches as accumulating snow pockets are released (London, 1908). Rocks, especially when they emerge aboveground, create uneven infiltration pockets, and also have complex thermal properties that result in small patches of condensation that can be tracked by root tips or microorganisms. They also redirect water flows creating complex water pockets, even to the extent of allowing the survival of mesic species within arid zones (Danin, 1999). Just as importantly, roots and microbes will accumulate where water pockets exist. Organisms then die back as water is depleted and rapidly grow into patches accumulating water. Water dynamics play especially crucial roles in managing and using arid and semi-arid regions for fiber and food production. Mediterranean and semi-arid climates served as the initial catalysts for the transition from gathering to agricultural economies. As the world's population continues to expand, many of these arid marginal habitats are of increasing importance, and are often the trigger points of human conflict. One important point is that the processes of water use and transport may not be different between mesic and arid areas, but the variance across time and space make these processes both more apparent (improving our ability to detect the dynamics) and ultimately more critical to maintaining plant growth and sustaining productivity.

Soil fungi are often treated as microorganisms because of their small diameter. That property allows them to exploit resources in tight spots, such as soil or rock pores. But a hypha can also extend several centimeters to several meters across a patch to find appropriate substrates, or in the case of mycorrhizal fungi, connect host plants with each other and with patchy soil resources. In one view, this makes mycorrhizal fungi integrators of soil patches for their host plants (Cui and Caldwell, 1996). Mycorrhizal fungi are mutualistic fungi associated with roots of 80% to 90% of plants globally, exchanging soil resources (nutrients, water) for carbon with host plants (Allen, 2007).

Fungi are not simply passive water consumers. Roots grow across soil textural boundaries and explore deep into the soil and even fractured rock to acquire water. Fungal hyphae penetrate into micropores and grow into rock matrices. In the process of penetrating pores, they provide straight edges for rapid water transport in contrast to the highly fractal pore surfaces often found in soil and rock pockets. In this paper, I will review what we have learned about complex water fluxes on a microscopic scale, and how those minute changes can catalyze processes critical to plant productivity and survival in arid conditions.

One final point is that the data and concepts for this paper are largely derived from our data from the Mediterranean-type forest and shrubland habitats of southern California, and a seasonal tropical forest in the Yucatan Peninsula. Precipitation is highly variable annually in both regions. In southern California, precipitation generally comes in the winter ranging from rain at lower elevations, to snow at higher. In the Yucatan Peninsula, the precipitation comes in late summer and especially during the autumn hurricane season. However, the physiological processes of plants and their mycorrhizal fungi are appropriate for any arid to semiarid region in which precipitation comes as distinct events, and are seasonally defined. This would include regions with monsoonal precipitation, the intensity of which varies from year-to-year. It is also important to note that these regions are often the source of water for agriculture and urban areas globally, and may well be the most sensitive regions to global climate change causing extensive problems in

water availability, storage, and allocation (IPCC, 2007).

1   Water infiltration and depletion in soils

Most useful models of precipitation, water depletion and irrigation focus on vertical movements of saturation zones. A layer of water is added to the soil surface, and modeled as it creates a saturation zone moving down through the soil profile. With enough precipitation or irrigation, the profile (or at least the rooting zone) is filled to holding capacity. Excess water then continues to flow through the soil, and into the groundwater layers. The upper surface will then evaporate, creating a surface depletion stratum. As roots extract water, water moves vertically to replace that loss, leading again to ever-deeper depletion layers, until the water levels go below the rooting zone. In irrigated agriculture or in mesic regions, the depletion zone rarely goes deep. For this reason, we can determine the amount of water that an irrigated crop will use, expressed in vertical mm to cm of water per day. In this way, water budgets and irrigation regimes are calculated.

Wildland ecosystems are characterized by horizontal as well as vertical patchiness in water input and use. Precipitation tends to infiltrate, initially filling macro-, then mesopores. Most of the micropores retain their moisture, down to very low levels of soil water. Infiltration, while complex, conceptually is reasonably well understood. Gravity and diffusion are the primary drivers. Channels along current roots or through past root- or animal (such as earthworms)-created gaps and surfaces define the directionality of that flow. Water moves vertically until it fills up pores and links with or forms groundwater pockets. Water also preferentially moves along surfaces such as rock interfaces, and in chaotic patterns across the soil surface, and into soil cracks and fractures. Channels form within soil resulting in a chaotic pattern of water infiltration (Jury *et al.*, 1991). With larger precipitation events, most of the pores re-fill, and a continuous water zone is created to groundwater (Hasselquist and Allen, 2009). In Mediterranean shrublands or deserts, most of the recharge occurs in heavy winter rains or snow. In tropical seasonally dry forests and summer precipitation deserts (such as the Sonoran in the southwestern U.S.) re-

charge occurs largely during the wet season, and often from tropical storms.

Water use by plants (evapotranspiration) is far more complex. Even in mesic ecosystems, water is preferentially used around each root, creating local depletion zones. Microbes grow in pockets of organic matter, where water is bound. This water has a lower water potential (ψ) when measured at the scale of most instrumentation, but not necessarily at the scales that microorganisms live. Individual root tips and mycorrhizal fungi extract water from soil pores. When water is adequate, macropores and mesopores are full. Water is extracted by plant roots from these pores. But as water is depleted from the larger pores, water stretches out forming a meniscus along soil particles. Droplets can be retained against solid surfaces and in smaller meso- and micropores. Under these circumstances, water may be accessed and transported along root hairs (for a small distance from the root surface) and then from mycorrhizal fungal hyphae (Allen, 2007) across macropores channels, and gaps (Fig. 1).
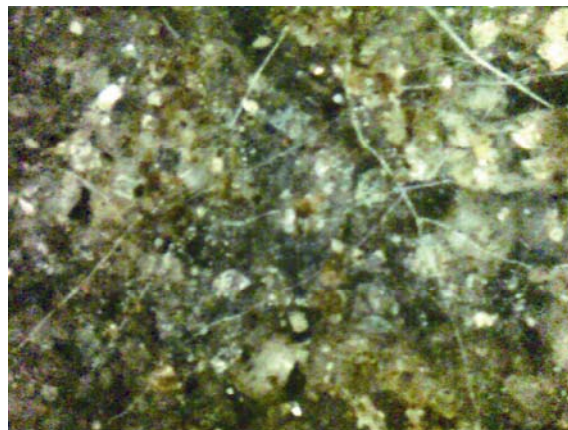

Fig. 1 Hyphae and soil particles from the automated minirhizotron (Allen *et al.*, 2007). Shown are arbuscular mycorrhizal fungal hyphae (knobby, dichotomously-branching) from the meadow site at the James Reserve. Also shown are the background soil particles, comprised of decomposed granite and pieces of organic matter. The site is a meadow within a California mixed-conifer forest, in a Mediterranean-type climate. Note the linear growth of the fungal hyphae that bridge soil pores and particles of varying sizes and chemistry.

It remains important to remember that this water infiltration and uptake is not a single dimension process, but occurs in all dimensions. This makes water extraction from soil extremely complex, and influenced by plant transpiration, evaporative demand, temperature

gradients, clay and organic matter types and content, root and fungal growth, distribution and connectivity, and other factors. Indeed, each site, and almost each patch must be measured and independently modeled to obtain a complete understanding of water and nutrient dynamics in arid ecosystems.

2 Patchiness in arid ecosystems

The ultimate limiting factor to productivity in arid regions is the amount of water and the length of the period of precipitation. High precipitation years, particularly El Nino years, can result in soil saturation and extend to the fractured granite underlying much of the southern California system. During drought years, the total input is less than required by the vegetation, so that groundwater, perched water tables, and even fractured granite serves as a water reservoir. Thus, the complex terrain coupled with highly variable water input creates both vertical and horizontal complexity in water distribution.

This distribution can be seen in vegetation. In southern California, Coast Live Oaks (*Quercus agrifolia*) will create stands in valley bottoms where the roots can reach the groundwater and exist as scattered trees on hillsides (Fig. 2). In the valley bottom stands, even during drought, trees are able to access the groundwater (Querejeta *et al*., 2009). On the hillsides, trees are dependent upon water stored in granite using roots to access the water in the fractures and mycorrhizal fungal hyphae to access water in the granite matrix (Egerton-Warburton *et al*., 2003; Bornyasz *et al*., 2005). Our isotope data (Allen, 2006) suggests that much of the water in the granite matrix ($\delta D = -52^o/_{oo}$) contains water accumulated during high precipitation years. This is because the δD results from the input of surface water from tropical storms, typical of wet years ($\delta D = -45^o/_{oo}$), compared with the water ($\delta D = -65^o/_{oo}$) from north Pacific storms prevalent during the drier winters (Querejeta *et al*., 2009).

Many arid lands (including southern California) have comparatively high soil nutrient levels. For example, southern California soils are of recent origin, and have relatively high levels of total P, K, Ca, and other essential nutrients. But, N is generally limiting as evidenced by the preponderance of legumes and actinorhizal perennial plants in arid ecosystems and

large plant responses to N fertilizer (Allen *et al*., 2009).

Fig. 2 Distribution of oak trees in Lopez Canyon, near Riverside, California. Trees in the stand (lower left) are located so that their roots can reach the groundwater. The scattered trees are found where roots cannot intercept groundwater, but instead use pockets of water and water in the decomposing granite (from Querejeta *et al*., 2009).

$\delta^{15}N$ values show the use of fixed N from desert legume trees (Shearer *et al*., 1983) to chaparral actinorhizal plants, such as *Ceanothus* spp. (Allen *et al*., 2005). During periods of adequate soil moisture, soil N limits production and patches where N is high, due to the presence of N-fixing symbiotic plants creates a complex soil nutrient patch structure. What this means is that any focus on carbon dynamics in arid lands needs to integrate both water and nutrient dynamics.

In these highly seasonal and patchy environments, roots continually explore the soil volume for water and nutrients. But as soils dry down, the distributions of nutrients and water diverge; more N nearer the surface litter, and water deeper. For this reason, one assumption generally made in ecosystem studies is that nutrients are primarily taken up during the wet period, and trees only access water, with minimal nutrient uptake during the dry period. However, as surface soils dry down, microbial mortality should also be high as litter increases. But fungal biomass estimates do not support this outcome (Allen, 2007). Fungal hyphae remain even in the driest soils (Allen *et al*., 2005). These surface soils also represent a large nutrient pool. This includes both the litter accumulation and aeolian

deposition. These accumulations are potentially important to plant growth. This would be especially important in that if these nutrients simply accumulated during the dry season, there would be a massive nutrient loss by leaching when the rains returned. This could especially have an impact on N, as nitrates are soluble and readily leached or denitrified under high soil moisture.

During the rainy season, roots grow rapidly using water and acquiring soluble nutrients in large soil pores (Kitajima *et al*., 2010). As the season warms and dries, roots deplete the available soil water from macro- and larger meso-pores. This creates a dry soil layer down through the rooting profile. At this point, we have observed that roots and their mycorrhizal fungi extend into fractures in the granite bedrock (Fig. 3) where there is water, but little in the way of nutrients. These roots form mycorrhizae and the hyphae from those mycorrhizae grow into the granite matrix (Egerton-Warburton *et al*., 2003; Bornyasz *et al*., 2005). Although these hyphae produce organic acids (Jurinak *et al*., 1986), our current observations suggest that hyphae primarily grow through this matrix mechanically by breaking through small fractures in the granite (Allen, unpublished observations).
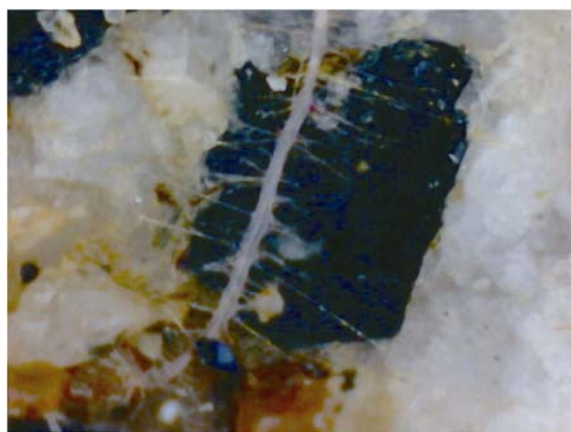

Fig. 3　A root with extending arbuscular mycorrhizal fungal hyphae, from the interior of a decomposing granite rock, exposed for approximately 160,000 years (Kitajima, Allen and Graham, unpublished observations).

As the soil dries down, micro-scale processes become important. Roots (and root hairs) have a limited range of pores in which they can penetrate. Root tips of shrubs and trees are generally 50 μm or larger. They can continue to pull some water along soil pores, but only until the water "bundles" become too thin to meet the uptake demands. Many species form ectomycorrhizae (EM), that is a form of mycorrhizal root tip in which the root cap of a short root is covered with a hyphal mantle. Hyphae and rhizomorphs (linear chords of hyphae ranging from a few to ten's of hyphae wrapped and even, for some taxa, enclosed in a hydrophobic casing) take up and transport water (Allen, 2007). In other plants, arbuscular mycorrhizae (AM) form structures internal to the root, just behind the region of elongation, with a hyphal network radiating out into the soil matrix (Allen, 1991). These hyphae are thinner than even root hairs (2 μm to 10 μm in diameter). Mycorrhizal hyphae also extend from a few cm to several m from the root. The small size of both EM and AM hyphae allow these fungi to access meso- and even larger micro-pores to access water (Allen, 2007). While at the scale of a total annual plant water balance, it may only represent a small fraction, during the dry down periods, this water may enhance drought tolerance and extend the plants growing season by up to a few weeks (Allen and Allen, 1986). This dry-down period also represents a period of high root mortality, and mycorrhizae may enhance root survival during these periods (Allen, unpublished observations).

To provide a contrast, we also studied the water sources in a seasonally dry tropical forest in the northern Yucatan Peninsula. Here, the extreme seasonality limits growth in the dry season, extending from January to June. Water levels drop as deep as 9 m, creating a dry zone and resulting in mostly deciduous trees. As there are a number of evergreen plants, we postulated that they were using ground water. However, to our surprise, in the northwestern part of the Peninsula (near Merida), isotopic analysis showed that none of the trees were using groundwater (Querejeta *et al*., 2006; 2007). All were using water found in pockets perched in the limestone (Fig. 4). Here, the water table appears to be disjunct from the plants. Just as interesting, these water pockets appear to fill during hurricane events (Estrada-Medina *et al*., 2010). The variable distribution of plants and water pockets means a high spatial and temporal variation in water resources. However, in the northeastern part of the Peninsula (at the El Eden Ecological Reserve), where the groundwater is shallow, and recharged by hurricane activity ($\delta^{18}O$ of $-4.2^o/_{oo}$), evergreen trees appear to utilize

deep water, even during the drought periods (Hasselquist *et al*., 2010). These two sites provide interesting contrasting hydrological regimes that merit further study. The northwestern part of the Peninsula is hydraulically disjunct from the remainder of the peninsula, associated with fracture zones created by the Chicxulub crater. The recharge is local, and can be associated with hurricane events (such as hurricane Isidore in 2002) that re-fill the groundwater (Hoddell *et al*., 2005). Groundwater drops dramatically (> 9 m) during the dry season and most roots do not appear to be able to tap this very deep water. There still may be exceptions to this pattern, as extremely deep roots in a mature forest were previously illustrated (Stephens, 1963). The northeastern region of the Peninsula, in Quintana Roo, Mexico, such as the El Eden Ecological Reserve, has underground rivers flowing northward. They are appear to be relatively shallow and can re-charge with both seasonal storms and following hurricanes, such as hurricane Wilma (Hasselquist *et al*., 2010).

Fig. 4 A pocket embedded in a limestone matrix, containing roots and mycorrhizal hyphae (with attached Ca crystals). This pocket was approximately 40 cm below the soil surface. The site is located near Merida, Yucatan, Mexico. These pockets contain water that is used by evergreen trees during the dry season (Querejeta *et al*., 2006). More details can be found in Estrada-Medina *et al*. (2010).

3   Integrating water and nutrient acquisition: hydraulic re-distribution and dynamic interaction

Roots and their symbiotic partners play critical roles in both temporal and spatial variable environments, accessing and redistributing water to optimize nutrient retention and uptake. During the dry season, a spatial segregation in soil resources exists; water deep, and nutrients shallow. Most ecosystem analyses assume that little nutrient uptake occurs; plants utilize deep water simply to maintain their resource base. However, during the night, when stomata are closed, water will move back into roots and into the soil in a process known as hydraulic lift (Richards and Caldwell, 1987). However, we found that if there are mycorrhizae in shallow, very dry soil, water will move from the plant, into mycorrhizal roots, then into the fungal hyphae. Specifically, deep-rooted oaks are able to take up deeper water through their taproots during the day. But, at night, instead of dumping it into the rhizosphere via hydraulic redistribution, that water was transported from the roots out into the mycorrhizal fungal hyphae (Querejeta *et al*., 2003).

Through this mechanism, mycorrhizal hyphae can be sustained even into very dry conditions (Querejeta *et al*., 2005; 2007). Because mycorrhizal fungal hyphae are hydrophilic near the tips, and hydrophobic through the main body, water can be transported long distances by this mechanism. Droplets with dyes of hydraulically lifted water can be seen emerging from hyphal tips at night (Fig. 5). These drops can take up N in extremely dry soils (Egerton-Warburton *et al*., 2008). Some of the water can even be transported to neighboring seedlings if the right fungal connections are made (Egerton-Warburton *et al*., 2007). This hydraulically lifted water also supports a network of EM fungi, trees, and even providing the water for fruiting of EM sporocarps (Warren *et al*., 2008; Lilleskov *et al*., 2009). The importance of these observations is that the deep water, even groundwater, or if in small pockets in fractured or dissolved bedrock, may be accessed by plants, and redistributed for sustaining microbial symbionts and for acquiring limiting nutrients near the soil surface. Deep water may even support seedlings during drought via hydraulic lift coupled and inter-plant hyphal transport (Allen, 2007; Egerton-Warburton *et al*., 2007).

Importantly, root symbiont interactions can be important in temporal as well as variable spatial dynamics, and previous "standardized" measurement techniques may provide misleading interpretations. For
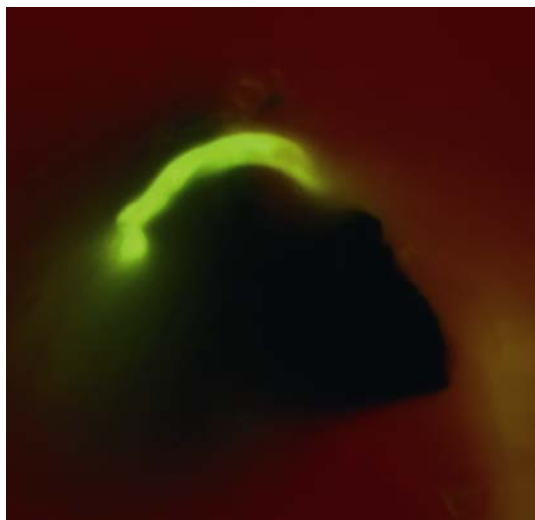
Fig. 5 A mycorrhizal fungal hyphal tip on a piece of organic matter with water containing a Lucifer Yellow carbohydrazide (LYCH) fluorescent tracer (from Allen, 2007). For details on the methods, see Querejeta *et al*. (2003).

example, Cui and Caldwell (1996) found that AM infection did not change in contrasting variable versus constant precipitation, and concluded that mycorrhizae had little to no role in nutrient uptake dynamics under these conditions. However, the root length increased with variable nutrient uptake; thus, the total numbers of mycorrhizal infection units per plant and per soil volume would have increased (Allen, 2001). Our previous data demonstrated that AM hyphae would persist into very dry conditions (Allen *et al*., 2005; Allen, 2006). Moreover, the nutrient that responded to the variable precipitation was ammonium, which was rapidly immobilized by the microbial biomass. Ammonium is not transported by mass flow and, therefore, like phosphate, is taken up by mycorrhizal fungi and transported to roots in arid systems (Ames *et al*., 1983). Also, a large fraction of the microbial biomass in these systems is likely to be AM fungal hyphae (Klironomos *et al*., 1999; Allen, 2001; Wilson *et al*., 2009). An alternative interpretation is that the increased numbers of roots with more variable precipitation resulted in greater numbers of mycorrhizal infection units. Since the AM fungal hyphae are efficient at absorbing ammonium, the fungal biomass rapidly accumulated the ammonium, and then slowly released it to the plant. This N was not leached because of the ability of the fungal hyphae to intercept the N (McFarland *et al*., 2010).

4   Implications for carbon exchange and sequestration

The importance of linking deep and surface waters goes well beyond the need for taking up water and nutrients for individual plants. Mycorrhizal hyphae represent an important long-term carbon sink. Most of the carbon fixed into mycorrhizae decomposes slower than fine roots and litter. Compounds such as glomalin (AM fungi) and chitin (all fungi) decompose slowly (Treseder and Allen, 2000). These compounds can comprise as much as 25% of the stable organic matter fraction (Wilson *et al*., 2009). With elevated CO_2, a greater fraction of the C is diverted to mycorrhizal fungi to enhance nutrient uptake to balance the increased C fixed (Allen *et al*., 2005), with concomitant increases in fungal carbon and soil aggregation (Rillig *et al*., 1999; Treseder *et al*., 2003). Thus, mycorrhizae access deep water, and, through roots, use the deep water to acquire surface nutrients. By sustaining mycorrhizal activity and photosynthesis during dry periods, more C is ultimately fixed and sequestered.

Just as importantly, accessing the deep water itself is both a root and microbial symbiont activity. Virginia *et al*. (1986) reported nodules with N_2-fixing symbionts deep into the groundwater (> 3 m) in desert legumes with AM fungi forming a layer just above the groundwater. Both AM and EM fungi have been observed growing into granite and limestone bedrock (Borynasz *et al*., 2005; Estrada-Medina *et al*., 2010). These deep hyphae also likely will not decompose rapidly, nor will the CO_2 diffuse rapidly back to the surface. These deep microbes may well form an important C sequestration mechanism, particularly in arid and semiarid regions. This hypothesis is supported by information on C fluxes in chaparral ecosystems (Allen *et al*., 2005; Luo *et al*., 2007).

Together, understanding the integral parts between plants, microbes, surface nutrients, and deeper water may be critical to understanding and managing both plant production in forest, shrubland and desert ecosystems, and may well hold important clues to optimizing irrigation agriculture in arid lands and in managing long-term atmosphere-soil carbon exchange.

5   Conclusions

Soils are comprised of the most complex diversity of

chemical and physical properties, biological organisms, and process per unit volume of any environment on earth. The biodiversity not only comprises incredible taxonomic diversity (tens of thousands of species/cm^3), but also an unbelievable array of biological structures, from ultrabacteria < 1 μm in diameter, to roots of the largest tree, to hyphae of mycorrhizal fungi and parasitic fungi that link to trees across multiple hectares of land, to animals as diverse as amoeba to vertebrates. Each of these organisms needs water to survive, and alter water flow patterns. Importantly, in the atmosphere, the most difficult factor to measure describing water fluxes is turbulence, requiring high temporal accuracy. In soil, the most difficult measurement is the pathway of water flow, or tortuosity.

Nevertheless, plants combined with their mycorrhizal symbionts require water and even direct water movement from the bedrock to the soil surface. Understanding the variation in soil patch structure combined with the range of regulatory processes and dynamics is critical to managing ecosystems ranging from grazing lands to irrigated agriculture. It is not only physical structure that dictates water movement patterns, but also the myriad of organisms, especially mycorrhizal fungi, that inhabit the interface between soil particles and plant roots. As we gain a better understanding of mycorrhizal fungi, roots, and soil structure, we should be better able to manage plant production in a changing global environment.

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