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Mycorrhizal relationships in bottomland hardwood forests of the southern United States

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Abstract

Mycorrhizae are important in the functioning of forest ecosystems worldwide, and play a critical role in water uptake, nutrient acquisition, and prevention of feeder root disease. The majority of mycorrhizal research has been conducted on upland sites, especially in coniferous ecosystems and in commercial agricultural production. However, the maintenance and restoration of bottomland hardwood (BLH) forest ecosystems in the southern United States is of increasing concern. Both ectomycorrhizae and endomycorrhizae are present in BLH forests, although the dominance of one or the other type depends primarily on both the tree species and the hydrologic regime. Ectomycorrhizae tend to be more sensitive to flooding, while endomycorrhizal infection can be present even in permanently flooded soils. The mycorrhizae of sweetgum (*Liquidambar styraciflua*), green ash (*Fraxinus pennsylvanica*), and the oaks (*Quercus* spp.) have been studied most due to their economic importance.

Considerable work is still needed to better understand mycorrhizal relationships in BLH ecosystems and associated trees, both with respect to infectivity and nutrient cycling. Such information may be necessary for restoration of BLH forests on old agricultural fields, or to maintain the productivity of BLH forests after harvest. This paper summarizes studies on mycorrhizae relationships in BLH forests and suggests future work necessary for understanding the role mycorrhizae can have in managing these ecosystems.

Introduction

Bottomland hardwood (BLH) forests comprise a significant portion of wetlands in the southern United States. Mitsch and Gosselink (1993) reported that in 1991, 4.9 million hectares of southern BLH forests remained of the original 21 million hectares estimated to have existed during Pre-Colombian times. Southern BLH forests are comprised of a diverse mix of tree species whose presence is generally restricted or controlled by site hydrology. Hydrology and nutrient flux also exert considerable influence on BLH productivity (Conner, 1994). The large oak (*Quercus* spp.) component of these communities provides significant amounts of hard mast for wildlife forage, thus making these forested wetlands extremely productive in terms of flora and fauna (Wigley and Roberts, 1994). In addition to wildlife habitat, BLH forests also serve an important role in flood attenuation, water quality maintenance, erosion control, and timber production (Taylor et al., 1990; Conner, 1994; Shepard, 1994).

Many of the tree species common to the BLH ecosystem are known to be mycorrhizal. Mycorrhizal roots (mycorrhizae) have an important role in the functioning of plant ecosystems. It is estimated that 85–90% of all terrestrial plants form mycorrhizae, and that nearly all woody plants are mycorrhizal (O'Dell et al., 1992). Many reviews

and summaries have been written on mycorrhizae development, mycorrhizae physiological relationships with fungi and plants, and the importance of mycorrhizae in plant ecology (e.g., Mosse et al., 1981; Allen, 1991, 1992; Francis and Read, 1994; Marshner and Dell, 1994; Pfleger and Linderman, 1994). However, the majority of studies on soil/mycorrhizae/plant relationships have been conducted on agricultural crops, temperate and boreal forests, dry upland sites, mine spoils, and in arid zones. In contrast, mycorrhizal dynamics in wetland ecosystems, and particularly BLH forests, have not been well studied, although they may have important roles in the functioning of these variable and complex ecosystems.

The purpose of this paper is to provide a synthesis of information on mycorrhizal relationships in wet forested ecosystems, with particular reference to BLH forests. This information will be important in understanding the role of mycorrhizae in the biogeochemistry of BLH ecosystems, and their importance in BLH ecosystem management and restoration.

Mycorrhizae

Mycorrhizae are plant root structures with absorption and biochemical attributes, which are formed by a mutualistic partnership between certain fungi and fine root tips. The fungi provide the root with increased surface area contact with the soil for nutrient and water absorption, while the mycorrhizal fungi are supplied with a source of carbon (sugars) fixed by the plant. Mycorrhizal fungi may also be important in soil organic matter breakdown, help protect the root from pathogens, and alleviate heavy metal toxicity (Mosse et al., 1981; Allen, 1991; George and Marschner, 1995).

The two main types of mycorrhizae, based on their morphology within the root, are ectomycorrhizae (EM) and endomycorrhizae, also called vesicular-arbuscular mycorrhizae (VAM). The EM fungi are mainly Basidiomycetes, familiar as the mushroom-forming fungi, while the VAM fungi are Zygomycetes, most of which form microscopic underground spores. Most EM fungi can be grown on agar media in pure culture, in contrast to VAM fungi, which are extremely difficult or impossible to grow in pure culture (Stribley, 1989; Dodd and Thomson, 1994). This characteristic becomes important in physiological studies on individual fungi, and in the production of fungal inoculum for laboratory and field colonization experiments.

The majority of plant species, including many trees, are colonized by VAM fungi, while EM are almost exclusively limited to woody species (Slankis, 1974; Mosse et al., 1981; Allen, 1991). Some plants can be colonized by both VAM and EM, but very few plants are non-mycorrhizal (Safir, 1987). Grasslands are characterized by VAM, temperate to boreal conifer forests are primarily EM, arctic biomes typically have ericoid mycorrhizae (a type intermediate between EM and VAM), tropical wetlands are mostly VAM, and BLH ecosystems are considered a complex mix of VAM and EM trees (Allen, 1991; Janos, 1992).

Soil nutrient uptake and cycling

Mycorrhizae generally contribute to plant health and vigor by increasing nutrient uptake, especially N and P (Slankis, 1974; Mosse et al., 1981; Allen, 1991; Marshner and Dell, 1994). This can be very important on sites where P and N are limiting. Mycorrhizal fungi do not fix atmospheric N, but may associate with N-fixing bacteria in or on the root (Mosse et al., 1981; Arnebrant et al., 1993). Laboratory and greenhouse studies have shown that EM can use organic forms of N (Abuzinadah and Read, 1989a, 1989b; Finlay et al., 1992), but whether this is relevant in field situations is unclear. VAM are associated with soil organic matter (Hepper and Warner, 1983), but it is not known if they play a role in organic matter breakdown. Both EM and VAM are important in the breakdown and transport of organic and inorganic forms of P (Bolan, 1991). In addition, K, Ca, S, Cu, Zn and Fe also are translocated to plants by one or the other of these mycorrhizae types (Marshner and Dell, 1994).

Mycorrhizal hyphae can also interconnect plants, which allows C, N, and P to be transferred between different root systems (Whittingham and Read, 1982; Finlay and Read, 1986; Allen, 1991; Eason et al., 1991; Arnebrant et al., 1993; Frey

and Schuepp, 1993). Because of the benefits bestowed to plants by mycorrhizal fungi, their role as "biofertilizers" has often been proposed (Stribley, 1989; Kropp and Langlois, 1990; Dodd and Thomson, 1994). Mycorrhizae inoculations have been shown to enhance seedling survival and growth, especially when indigenous mycorrhizae have been disturbed by mining, long-term monocropping, or pesticide use (Safir, 1987; Marx and Cordell, 1988; Abbott and Gazey, 1994).

However, the benefits conferred to plants by mycorrhizal fungi do not come without a cost to the host. Allen (1991) gave 25% as an average value for the amount of fixed carbohydrate a plant invests in its mycorrhizal partner, although values from 10–40% have been reported. While most studies have shown beneficial effects of EM on nutrient uptake and plant growth, they occasionally may cause little or even a negative growth response (Bledsoe et al., 1982; Gagnon and Langlois, 1987; Nylund and Wallander, 1989; Osonubi et al., 1991). In these situations the energy costs for mycorrhizal seedlings to maintain fungal hyphae and greater numbers of fine roots outweigh the benefits derived from increased nutrient uptake, although non-nutritional benefits to plants by mycorrhizal infection may still be an advantage. Growth reductions caused by mycorrhizal fungi under some soil conditions are usually more than offset by increased seedling survival (Harvey et al., 1986).

Soil/plant water relations

Many studies have shown that both VAM and EM enhance water uptake, especially in arid soils (e.g., Read, 1985; Boyd et al., 1986; Andersen et al., 1988). Faber et al. (1991) demonstrated a role in transport of water to the host plant by mycorrhizal hyphae. Boyd et al. (1986) noted a 40% decline in transpiration in birch and pine seedlings when EM mycelial strands were cut. The mycorrhizal extramatrical mycelium essentially becomes an extension of the plant root system, exploring and translocating more water and nutrients than the root could by itself (Read, 1985). Plants colonized by VA mycorrhizal fungi generally show greater drought resistance than non-mycorrhizal plants (Sylvia and Williams, 1992).

In contrast, mycorrhizal research in soils where water is not limiting, or is in excess, has generally been neglected. Numerous studies have been conducted on the effects of low soil oxygen levels on various aspects of plant growth and development, but few indicated whether the plant roots were colonized by mycorrhizal fungi (Read, 1985; Pezeshki, 1994). Although some wetland plants are known to be non-mycorrhizal, such as sedges (*Carex* spp.), rushes (*Juncus* spp.), and horsetails (*Equisetum* spp.), many others are mycorrhizal (Safir, 1987; Kühn, 1991; Rickerl et al., 1994). It is generally assumed that terrestrial plants decrease their mycorrhizal dependency as soil conditions get wetter (O'Dell et al., 1992). For example, roots of *Populus euroamericana* L. growing on stream banks were nonmycorrhizal, while roots growing in nearby drier soil had both EM and VAM (Shuja et al., 1971).

Mycorrhizal fungi are aerobic organisms, and therefore, high soil moisture levels and resultant oxygen limitations would make it more difficult for mycorrhizal fungi to infect plant roots (Slankis, 1974; Stenstrom, 1991; Khan, 1993). However, Mosse et al. (1981) indicated soil water usually contains sufficient dissolved oxygen to prevent total anoxia, even under flooded conditions. The response to such soil water excess appears to vary considerably between EM and VAM (Mosse et al., 1981). The difference in taxonomic class of EM and VAM fungi may partially account for such variability in tolerance to high soil water levels. Vesicular-arbuscular mycorrhizae are formed by the more primitive Zygomycetous fungi, which may be better able to tolerate saturated soil conditions. In contrast, EM are formed by higher fungi (Basidiomycetes), and are often adapted to drier environmental conditions.

Ectomycorrhizae (EM)

Ectomycorrhizae are generally more sensitive to soil water content than VAM, which occur from arid regions to permanently waterlogged marshes (Mosse et al., 1981; Allen, 1991). However, EM fungi exhibit a range of tolerance to flooding and soil water potential. Certain EM fungi (*Hebeloma*,

Laccaria, *Thelephora*) colonizing Scots pine seedlings were more tolerant to periodic flooding than others (*Suillus*), which failed to form mycorrhizae when roots were flooded for just two minutes per day (Stenstrom, 1991). Similarly, when Coleman et al. (1989) tested 18 species of EM fungi in vitro to impose water stress, a range of tolerance was found, as well as considerable strain variation among individual species. Ectomycorrhizal fungus species also show considerable variation in their ability to survive long-term storage in water, and they are generally more susceptible to death by submersion than species of saprotrophic fungi (Richter and Bruhn, 1989).

Tree growth also seems to reflect EM/soil water content relationships. Bougher and Malajczuk (1990) reported that inoculation with EM fungi increased the growth of karri seedlings (*Eucalyptus diversicolor* F. Muell.) under a range of soil moisture conditions, compared to uninoculated seedlings. However, EM numbers were reduced as soil moisture increased, until no growth differences were found between the inoculated and the uninoculated seedlings at soil saturation. Gadgil (1972) reported reduced P and enzymatic activity in EM roots of both radiata pine (*Pinus radiata* D. Don) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), which were waterlogged for 16 weeks, but the EM of Douglas-fir were more negatively impacted than those of radiata pine.

Vesicular-asbuscular mycorrhizae (VAM)

While VAM are more tolerant to soil water excess than EM, their infection rate is generally reduced as soil moisture content increases (Khan, 1974, 1993; Reid and Bowen, 1979; Mosse et al., 1981; Solaiman and Hirata, 1995). However, once established, VAM may endure prolonged flooding, and some VAM infection can even occur at soil saturation (Khan, 1993; Rickerl et al., 1994). The lowest VAM colonization of three native herbs along a toposequence in Ohio were in the lowlands, where soil moisture was highest (DeMars and Boerner, 1995). Likewise, Rickerl et al. (1994) found a steady decrease in VAM infection rate of wetland plants going from dry to wet sites. While lower levels of oxygen are the likely cause for this VAM decrease, mycoparasitism by certain mobile, parasitic fungi (Chitrids) in waterlogged soils may also limit populations of VAM fungi (Jeffries, 1995).

Bottomland hardwood forests

The wettest sites in southern BLH forests are along stream and river banks, which are frequently flooded. These sites are dominated by *Taxodium* and *Nyssa* species. Where flooding occurs less often, overcup oak (*Quercus lyrata* Walt.), water hickory (*Carya aquatica* (Michx.) Nutt.), green ash (*Fraxinus pennsylvanica* Marsh.), red maple (*Acer rubrum* L.), black willow (*Salix nigra* Marsh.), cottonwood (*Populus deltoides* Bartr.), and river birch (*Betula nigra* L.) are common associates. With somewhat drier conditions, several species of oaks (*Q. laurifolia* Michx., *Q. rubra* L., *Q. phellos* L.) predominate along with American elm (*Ulmus americana* L.), sweetgum (*Liquidambar styraciflua* L.), hackberry (*Celtis laevigata* Willd.), and sycamore (*Platanus occidentalis* L.). Loblolly pine (*Pinus taeda* L.) and spruce pine (*Pinus glabra* Walt.) may also occur in mixed pine-hardwood stands. At the upper elevations of the floodplain where the chance of flooding is slight, cherrybark oak (*Q. falcata* var. *pagodifolia* Ell.), swamp chestnut oak (*Q. michauxii* Nutt.), and water oak (*Q. nigra* L.) are important forest components (Wharton et al., 1982).

As noted earlier, the importance of mycorrhizae in many aspects of plant growth and development has been shown for many different types of ecosystems. However, a review of literature of the past 25 years has indicated relatively little work has been conducted on the mycorrhizae of BLH tree species, or how they may affect the functioning of this ecosystem (Table 1). Most of this research has concentrated on sweetgum and green ash, both of which are important forestry and horticultural species. In contrast, no mycorrhizal studies were found on river birch, hackberry (*Celtis* spp.), diamondleaf oak (*Q. laurifolia*), swamp chestnut oak, and American elm. Of the 14 BLH tree species which have been studied, 5 form VAM, 2 form EM, and 7 can have both mycorrhizal types.

Table 1. Mycorrhizal research on selected bottomland hardwood tree species reported in the literature.

Tree species	Ecological zone[1]	Mycor. type	Citations
Acer rubrum	II	VAM	Kormanik et al., 1982; Schultz and Kormanik, 1982
Fraxinus pennsylvanica	II	VAM	Borges and Chaney, 1989, 1993; Lamar and Davey, 1988; Andersen et al., 1987, 1988; Douds and Chaney, 1982, 1986; Pope et al., 1983; Kormanik et al., 1982; Schultz and Kormanik 1982; Schultz et al., 1981; Riffle, 1980
Nyssa sylvatica	II	VAM	Keeley, 1980
Salix nigra	III	EM, VAM	Lodge, 1989; Antibus et al., 1980
Quercus lyrata	III	EM	Filer, 1975
Populus deltoides	III, IV	EM, VAM	Lodge and Wentworth, 1990; Lodge, 1989; Vozzo and Hacskaylo, 1974
Plantanus occidentalis	III, IV	VAM	Pope et al., 1983; Kormanik et al., 1982; Schultz and Kormanik 1982; Schultz et al., 1981
Carya spp.	III, V	EM, VAM	Richter, 1995[2]; Sharpe and Marx, 1986; Woodroof, 1933
Liquidambar styraciflua	IV	VAM	Kormanik, 1986, 1985; Pope et al., 1983; Kormanik et al., 1981, 1982, 1977; Simmons and Pope, 1987, 1988; Schultz and Kormanik, 1982; Schultz et al., 1979; Filer, 1975
Quercus phellos	IV	EM	Richter, 1995[2]; Filer, 1975
Quercus falcata	V	EM, VAM	Beckjord et al., 1983; Grand, 1969
Quercus falcata var. *pagodifolia* (= *Q. pagodifolia* and *Q. pagoda*)	V	EM,VAM	Richter, 1995[2]; Beckjord et al., 1983
Quercus nigra	V	EM, VAM	Richter, 1995[2]
Quercus nuttallii	–	EM, VAM	Richter, 1995[2]; Filer, 1975

[1]After Wharton et al., 1982. (II = wettest, V = driest)
[2]Unpublished data

The factors influencing the development of mycorrhizal types on different BLH trees are not fully understood. The distribution of mycorrhizae among families of vascular plants varies considerably; even closely related species can differ in their association with either VAM or EM (Newman and Reddell, 1987). Watson et al. (1990) reported that oak species in the red oak group (Erythrobalanus) were able to form either EM or VAM. Red oaks growing on lowland sites had more VAM root tips, while those growing on upland sites had more EM. However, each type of mycorrhizae could be found at wet or dry sites. In contrast, the white oak group (Leucobalanus) only form EM, regardless of soil moisture conditions.

Mycorrhizae occurrence

Very little is known about the tolerance of BLH mycorrhizae to wet soil conditions, but the few studies conducted show reduced mycorrhizae numbers in wetter soils. Colonization of black gum (*Nyssa sylvatica* Marsh.) roots by VAM was less in flooded soil than in non-flooded soils, but they were still infected after a year of waterlogging (Keeley, 1980). VAM infection rates also decreased as distance from main roots increased, which indicated that internal root oxygen transport in black gum may limit mycorrhizal development. Red oak EM were substantially reduced under high soil moisture levels (Watson et al., 1990). Under the very wet conditions typical of fine-textured BLH soils, poor aeration may restrict mycorrhizal development in deeper soil horizons. Mycorrhizal infection on these sites may also be influenced by individual tree species tolerance to waterlogging. This is especially true for trees that form internal aeration systems (lenticels and aerenchyma) that allow oxygen diffusion from the stem to the roots (Hook, 1984; Pezeshki, 1994). Similar diversity in EM tolerance to waterlogging was also found in several old-growth BLH sites (unpublished data, D.L. Richter). Surprisingly, the

Table 2. Total VAM spores in soil cores from three old-growth bottomland hardwood sites, and one bottomland old field site (expressed as number of spores per 100 g of dry soil).[1]

Depth (cm)	Coosawhatchie River (South Carolina) Forest	Cache River (Arkansas) Forest	Lake George (Mississippi)	
			Forest	Old Field
0–5	2032	760	1127	581
5–10	1348	526	548	261
10–15	764	570	383	212
15–20	465	431	223	255
20–30	444	677	164	208

[1]Unpublished data (Richter 1995). Samples taken in June/July 1995. Spores extracted using the method of Vilarino and Arines (1990).

well known and nonspecific EM fungus, *Cenococcum graniforme* (Sow.) Ferd. & Winge, usually reported as characteristic of dry sites (Read and Boyd, 1986), was commonly encountered on oak and hickory roots on their sites.

The number of VAM spores in soil is often considered an indicator of root mycorrhizal infection (Mosse et al., 1981; Daniels Hetrick, 1984), although spore production may be more important for dispersal during environmental stress (Allen, 1991). Preliminary results from old-growth BLH sites in Arkansas, Mississippi and South Carolina showed high numbers of VAM spores (500 to 2000/ 100 g of soil) in the surface 10 cm mineral soil layer (Table 2). Numbers of spores reported from other wetland soils range from <1 to 500/ 100 g of soil (Janos, 1992; Rickerl et al., 1994). Considerable differences in spore size and color were found in the BLH soils, which indicates VAM species differences among these BLH sites. As expected, VAM spore numbers decreased as soil depth increased, following trends similar to other soil microorganisms. However, VAM root infection may not always relate to spore numbers in the soil due to spore dormancy, the presence of other infective propagules (e.g., hyphal contacts), and the difficulty of counting spores in the soil (Abbott and Robson, 1991).

Seasonal variation in VAM spore numbers and root infection rates has been reported for green ash seedlings (Douds and Chaney, 1986). Such variability during the growing season can be a function of plant phenology (Abbott and Robson, 1991; Wetzel and van der Valk, 1996), but it may also reflect soil moisture levels at that time of the year. High soil moisture content or free water movement is not usually necessary for the spread of VAM spores, but they do require a certain amount of soil moisture to retain viability (Ruiz-Lozano and Azcon, 1996). Adequate water is also necessary for infection by hyphal growth from roots, and for root to root contact. Also, many VAM and EM are dependent on small mammals and soil fauna for spore dispersal (Mosse et al., 1981; Allen, 1991).

Ecological significance

From the previous discussion, it is evident that mycorrhizae are a component of BLH root systems, even on very wet sites. However, the ecological function of VAM or EM in BLH ecosystems is not clear. Mycorrhizae are important in water uptake on upland forested sites, but their contribution in BLH soils may depend on the depth of the water table during the growing season, and the extent of the capillary fringe. Increased water uptake by mycorrhizae could be a factor in tree establishment and productivity in exceptionally dry years, or at the upper edges of the flood plain.

Mycorrhizae will likely contribute to nutrient uptake on BLH sites, but the relationship would be different than in drier soils. With high soil moisture levels, more nutrients would move to the plant roots by diffusion and mass flow in response to evapotranspiration losses. Increased movement

of N to roots could be balanced by greater N losses from denitrification on some sites (Walbridge and Lockaby, 1994). The increased soil-root contact provided by both VAM and EM would still be very important for P uptake in wet soils, since very little P moves to the plant by mass flow. Although P becomes more available if the soil redox conditions are low enough to change Fe^{+3} to Fe^{+2}, moderately tolerant BLH species often show P deficiencies in waterlogged soils (McKevlin et al., 1987). How mycorrhizae contribute to P uptake in such very wet soils is not known.

Forest management implications

Clearcut harvesting followed by natural regeneration is the most common silvicultural technique used in BLH forests (Conner, 1994). Clearcut systems usually use mechanized, ground-based harvest machinery, which often causes increased soil bulk density, and decreases hydraulic conductivity and redox potential on these wet sites (Walbridge and Lockaby, 1994). How these forest management-related changes in soil properties will impact BLH mycorrhizae and their effect on subsequent seedling establishment and growth is unclear.

Increased soil bulk density caused decreased root growth and incidence of VAM in sweetgum seedlings (Simmons and Pope, 1987). However, even the presence of low VAM numbers reduced the negative effects of soil compaction. VAM formation can also be reduced by the mixing or disruption of soil horizons, such as may occur with mechanical harvesting of forested sites and in mine reclamation practices (Stahl et al., 1988; Jasper et al., 1991). The degree by which soil disturbance affects VAM formation depends on the relative abundance of spores, mycorrhizal roots, and fungal hyphae in the soil (Hepper and Warner, 1983). The lower the VAM spore numbers, the more VAM development will depend on existing VAM roots and hyphae, both of which are more sensitive to soil disruption (Jasper et al., 1989).

Little information is available on the occurrence of VAM propagules on BLH sites before or after harvest. Compared to an adjacent old-growth BLH forest, numbers of VAM spores were much lower in an old agricultural field, which is part of BLH restoration program (Table 2). It would seem unlikely that a lack of VAM spores on this site would affect the re-establishment of BLH, since spore numbers were still quite high when compared to other wetland soils (Rickerl et al., 1994). However, changes in soil chemical and physical properties as a result of harvesting or other site disturbances could reduce the effectiveness of the VAM fungi originally adapted for the site (Stahl et al., 1988).

Clearcutting also increases soil temperature and adds large amount of logging residue to the soil surface, which results in increased organic matter decomposition and mineralization of N and P (Aust and Lea, 1991; Lockaby et al., 1997). As discussed earlier, increased nutrient availability in wetland soils after harvesting could reduce the need for mycorrhizae in nutrient uptake. Consequently, the occurrence of lower mycorrhizae numbers after harvesting BLH sites as a result of soil compaction or elevated water table may only have minimal impact on soil nutrient uptake. However, studies are still needed to verify or disprove this possibility.

Conclusions and perspective

The benefits of mycorrhizal infection on tree growth and development has been clearly shown for forested, upland sites. However, this is not the case for the very wet BLH ecosystems, which are strongly influenced by periodic flooding. Both EM and VAM are present in BLH root systems, but certain tree species have a requirement for either EM or VAM. Some BLH tree species, such as oaks and hickories, can form partnerships with both EM and VAM, although the factors influencing the incidence of mycorrhizal type among plants is not fully understood. Increasing levels of soil water generally favors VAM over EM, but the numbers of both mycorrhizal types are usually reduced. What this would mean for tree nutrient and water uptake on wet sites is unclear. Reduction of BLH mycorrhizae due to high soil moisture content could limit nutrient uptake, but conversely, increased nutrient availability in some soils may reduce the need for mycorrhizae. The

carbon cost to maintain mycorrhizae on BLH root systems may only provide maximum benefit to trees during periods of low soil moisture conditions.

Timber harvesting of BLH forests can cause significant changes in soil physical and chemical properties, which could negatively impact mycorrhizae development. Whether such changes in mycorrhizal types or numbers will affect seedling establishment and growth, or subsequent site productivity is unknown. Little information is available on the numbers and suitability of mycorrhizae in soils which are targeted for BLH restoration.

Considerable work needs to be done to characterize the mycorrhizal relationships of individual BLH tree species. Most of the research that has been done involves a few trees that are important to forest industry and horticultural practice. Very little is known about the dynamics of native fungi forming VAM and EM in natural BLH forests and their effect on soil processes. The importance of mycorrhizae for the uptake and transfer of C and nutrients among different tree species in BLH ecosystems also needs to be determined, and how these processes are affected by forest management practices. Information on mycorrhizal fungi in old agricultural fields that may be restored to BLH forests is needed, since they may be different than indigenous mycorrhizae of the original BLH forests. Such information may be necessary for restoration of BLH forests on old agricultural fields, or to maintain the productivity of BLH forests following harvest.

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