

Mycorrhizal Associations and Plant Propagation

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INTRODUCTION

All plants of commercial or ecological value can have their "roots" traced back to the forest. All we have done is collect them from the forest, propagate them in some fashion and then plant them in various manmade environments, such as tree plantations, orchards, roadsides, urban landscapes, shopping centers, and pots in the patio. Regardless of where these plants are now growing, they still have the genetic requirements they acquired over some 300 million years of development in forests. Most of these requirements are related to the soil. Forest soils typically have a well-defined surface layer of organic litter, large porous channels caused by roots and animal activity, high amounts of decomposing organic matter, and an accumulation of woody debris on the surface. Most of these characteristics are missing in man-made environments. The perennial root systems of most forest plants support diverse macro- and microorganisms in the forest floor, soil, and rhizosphere (i.e., fine root surfaces). The organisms disintegrate and decompose organic matter, and then release (recycle) the nutrient elements for eventual re-absorption by forest vegetation. Nutrient and water absorption by forest plants is synchronous and interdependent.

Large amounts of essential plant elements, i.e., N, P, K, Ca, Mg, Fe, Zn, etc., are bound and unavailable to plants in the organic matter and mineral components of the forest soil. Only small amounts of these inorganic elements are made available in soil solution by microbial activity at any specific time. In temperate forest soils, rarely are there more than 5 to 10 ppm of either available inorganic N or soluble P in soil solution at any time during the growing season. Forest plants have evolved biological systems or "partners" to assure them of adequate supplies of these essential elements from soils of low fertility.

Microorganisms are abundant on or near the fine absorbing roots of forest plants and they play vital roles in numerous physiological and chemical processes. These dynamic processes are mediated by activities of microorganisms participating in saprophytic, pathogenic, and symbiotic associations on roots of forest plants. Certain species of saprophytic bacteria oxidize mineral elements, like P, into soluble forms, fix atmospheric N, stimulate root growth by producing plant growth regulators, act as biological deterrents to root-disease causing microbes, and decompose man-made organic chemicals in the rooting zone.

MYCORRHIZAE

The most widespread symbiotic association on roots of forest plants is mycorrhiza (fungus-root). The term mycorrhiza is used to describe a structure that results from a mutually beneficial association between the fine absorbing roots of plants and species of highly specialized, root-inhabiting fungi. The mycorrhizal fungi derive most, if not all, of their needed organic nutrition (carbohydrates, vitamins, amino acids) from their symbiotic niche in the primary tissues of absorbing roots. Evidence

suggests that the mycorrhizal habit has evolved as a survival mechanism for both partners in the association, allowing each to survive in the existing forest environments of low soil fertility and water, disease, and temperature extremes. Because of this coevolutionary process, mycorrhizae are as common on the root systems of forest plants as are chloroplasts in their leaves. In examining forest plants in a natural environment, the question should not be "are these plants mycorrhizal" because they all are, but rather "what type of mycorrhiza is present and what is the degree of mycorrhizal development on the roots"?

Endomycorrhizae. This type of mycorrhiza is the most widespread and comprises three groups. Ericaceous mycorrhizae occur on four or five families in the Ericales and include *Rhododendron*, laurel (*Kalmia*), cranberry (*Vaccinium macrocarpon*), and blueberry (*Vaccinium*). Orchidaceous mycorrhizae are a distinct type that occur only in the plant family Orchidaceae. These two groups of endomycorrhizae are not widespread and will not be discussed further. Vesicular-arbuscular mycorrhizae (VAM) form the third group of endomycorrhizae. Vesicles and arbuscules are structures produced by the endomycorrhizal fungus in or on roots. VAM occur on more plant species than all other types of mycorrhizae combined and have been observed in roots of over 1000 genera of plants representing some 200 families. It has been estimated that over 90% of the 300,000 species of vascular plants in the world form VAM. These include agricultural crops, turfgrass, fruit and nut trees, most hardwoods, vines, desert shrubs, flowers, and woody ornamentals. VAM fungi are ubiquitous in all natural soils except where they have been eliminated by prior land-use practices. Inoculum density and fungal species diversity, however, vary greatly in different soils supporting different plants. There are about 150 species of VAM fungi identified to date. None can be grown in pure culture in the laboratory. VAM fungi cannot grow saprophytically in soil and, therefore, will only grow while in symbiotic association with their plant hosts. They may, however, survive for decades in soil as dormant spores without plant associations. VAM roots are not changed in either color, shape or form as are ectomycorrhizae. VAM can only be confirmed microscopically.

VAM increase a plant's uptake of water and certain nutrients, particularly P, Cu, and Zn. These elements are relatively immobile in soil, and zones of depletion normally develop near absorbing roots. The extramatrical growth of hyphae from VAM fungi extends beyond the absorbing roots and, thereby, increases the volume of soil from which these elements are absorbed. The additional nutrient and water absorption capability due to VAM can result in several-fold growth increases in plants.

There are other significant benefits of VAM to plants. VAM are capable of increasing plant resistance to various fungal root pathogens and parasitic nematodes. VAM have also been shown to enhance water uptake, increase tolerance to heavy metals, saline soils and drought, decrease transplant shock, and bind soil into semistable aggregates.

Ectomycorrhizae. This type of association occurs on about 10% of the world flora. Trees belonging to the Pinaceae (pine, fir, larch, spruce, hemlock), Fagaceae (oak, chestnut, beech), Betulaceae (alder, birch), Salicaceae (poplar, willow), Juglandaceae (hickory, pecan), Myrtaceae (*Eucalyptus*), Ericaceae (*Arbutus*), and a few others form ectomycorrhizae. Some tree genera, such as *Alnus*, *Eucalyptus*, *Casuarina*, *Cupressus*, *Tilia*, *Ulmus*, and *Arbutus* can form both ectomycorrhizae and VAM,

Table 1. A few of the plants that are known to benefit from mycorrhizal fungal manipulations.

Ectomycorrhizal Forest and Urban Trees		
birch 4 spp. (<i>Betula</i>)		
cedrus 2 spp. (<i>Cedrus</i>)		
cottonwood (<i>Populus</i>)		
<i>Eucalyptus</i> 4 spp		
fir 3 spp. (<i>Abies</i>)		
hemlock 2 spp. (<i>Tsuga</i>)		
larch (<i>Larix</i>)		
oak 9 spp. (<i>Quercus</i>)		
pecan (<i>Carya illinoensis</i>)		
pine 27 spp. (<i>Pinus</i>)		
poplar (<i>Populus</i>)		
spruce 4 spp. (<i>Picea</i>)		
VAM Forest and Urban Trees		
ash 2 spp. (<i>Fraxinus</i>)		
cypress (<i>Taxodium</i>)		
empress tree (<i>Paulownia</i>)		
gums 3 spp.		
Leyland cypress (XCupressocyparis leylandii)		
maples (<i>Acer</i>)		
magnolia (<i>Magnolia</i>)		
palm (<i>Elaeis</i>)		
redbud (<i>Cercis</i>)		
redwood (<i>Sequoia</i>)		
sycamore (<i>Platanus</i>)		
	VAM Fruit, Nut, Vine and Berry Plants	
	apple (<i>Malus</i>)	lespedeza (<i>Lespedeza</i>)
	avacado (<i>Persea</i>)	ryegrass (<i>Lolium</i>)
	banana (<i>Musa</i>)	sunflower (<i>Helianthus</i>)
	blackberry (<i>Rubus</i>)	switchgrass (<i>Panicum</i>)
	cherry (<i>Prunus</i>)	VAM Ornamentals
	cocoa (<i>Theobroma</i>)	aster (<i>Aster</i>)
	citrus (<i>Citrus</i>)	barberry (<i>Myrica</i>)
	coffee (<i>Coffea</i>)	bearberry (<i>Arctostaphylos</i>)
	grape (<i>Vitis</i>)	boxwood (<i>Buxus</i>)
	mango (<i>Mangifera</i>)	chrysanthemum (<i>Dendranthema</i>)
	olive (<i>Olea</i>)	dogwood (<i>Cornus</i>)
	papaya (<i>Carica</i>)	geranium (<i>Geranium</i>)
	peach (<i>Prunus persica</i>)	hibiscus (<i>Hibiscus</i>)
	pear (<i>Pyrus</i>)	hydrangea (<i>Hydrangea</i>)
	pineapple (<i>Ananas</i>)	hawthorn (<i>Crataegus</i>)
	pistacia (<i>Pistacia</i>)	juniper (<i>Juniperus</i>)
	plum (<i>Prunus</i>)	lily (<i>Lilium</i>)
	raspberry (<i>Rubus</i>)	marigold (<i>Tagetes</i>)
	strawberry (<i>Fragaria</i>)	pittosporum (<i>Pittosporum</i>)
		poinsettia (<i>Euphorbia</i>)
		privet (<i>Ligustrum</i>)
		rose (<i>Rosa</i>)
	VAM Grasses, Legumes, etc.	VAM Transplanted Field Crops
	bahiagrass (<i>Paspalum notatum</i>)	asparagus (<i>Asparagus</i>)
	bluegrass (<i>Poa</i>)	peppers (<i>Capsicum</i>)
	bentgrass (<i>Agrostis</i>)	tobacco (<i>Nicotiana</i>)
	clover (<i>Trifolium</i>)	tomatoes (<i>Lycopersicon</i>)
	centipede grass (<i>Eremochloa</i>)	

depending on the soil conditions, tree age, and availability of mycorrhizal fungal inoculants.

Numerous fungi have been identified as forming ectomycorrhizae. In North America alone it has been estimated that more than 2100 species of fungi form ectomycorrhizae with forest trees. Worldwide, there are over 5000 species of fungi that can form ectomycorrhizae on some 2000 species of woody plants. Most of these fungi produce mushrooms or puffballs. However, less than 20 percent of the mushroom or puffball-producing fungi are mycorrhizal, the majority are saprophytic litter and wood decomposers in the forest.

In ectomycorrhizae, intercellular hyphae surround cortical cells forming the Hartig net, and several hyphal layers cover the outside of the feeder root forming the fungus mantle. Ectomycorrhizal colonization normally changes the feeder root morphology and color. They may be unforked, bifurcate, nodular, multi-forked (coralloid), or other shapes. Their color, which is usually determined by the color of the mycelium of the fungal symbiont, may be jet-black, red, yellow, brown, white, or blends of these colors. Unlike VAM, many ectomycorrhizal fungi can be grown routinely in pure culture in the laboratory. An important aspect of both VAM and ectomycorrhizal fungi is that neither group can grow saprophytically in nature, they can only grow while in the plant root association. Spores or other resistant structures of the fungi, however, may survive long periods in soil without a plant host.

Ectomycorrhizal fungi aid the growth and development of trees. For some trees, such as *Pinus*, they are indispensable for growth under natural conditions. The obligate requirement of pine for ectomycorrhizae in a natural environment has been clearly shown by numerous workers in tree regeneration trials in former treeless areas and in countries without native ectomycorrhizal trees. Trees with abundant ectomycorrhizae have much larger, physiologically active, root-fungus area for nutrient and water absorption than trees with few or no ectomycorrhizae. This increased absorptive surface area is a combination of the multi-branching habit of most ectomycorrhizae and the extensive vegetative growth of fungal hyphae from the ectomycorrhizae into the soil. As with VAM, these extramatrical hyphae function as additional nutrient and water-absorbing entities and promote maximum nutrient and water capture from the soil by the host plants. Ectomycorrhizae have been shown to increase the absorptive surface of root systems of 4-month-old pine by over 700% when compared to nonmycorrhizal roots. Ectomycorrhizae are also able to absorb and accumulate more N, P, K, and Ca in the fungus mantles, more rapidly, and for longer periods of time than nonmycorrhizal roots. They also increase the tolerance of trees to drought, high soil temperatures, soil toxins (organic and inorganic), and extremes of soil-acidity caused by high levels of sulfur or aluminum. They also function as biological deterrents to root pathogens, such as species of *Pythium* or *Phytophthora*, and to parasitic nematodes. Plant hormone relationships induced by fungal symbionts result in ectomycorrhizal roots having greater longevity (length of physiological activity) than nonmycorrhizal roots. Not all species of fungi form ectomycorrhizae that have equal benefit to their hosts; some are more effective than others.

PRACTICAL CONSIDERATIONS

Over 20,000 research papers have been published on mycorrhizae since the turn of the century. A considerable amount of this research has been done on the response

of plants to mycorrhizal fungus inoculations under a variety of test conditions. Table 1 shows just a few of the plants that are known to benefit from mycorrhizal fungal manipulations. Many others are not listed because of limited space. These results should not be surprising since they are all forest plants and mycorrhizae have been the natural state of their absorbing roots in forest soils for millions of years. Unfortunately, our modern-day plant propagation practices discourage the natural occurrence of abundant mycorrhizae. Artificial potting mixes and sterilized (fumigated/steamed) soils contain few, if any, propagules of mycorrhizal fungi. High fertility and frequent irrigation also discourage mycorrhizal development even if adequate fungal propagules are present. Research has repeatedly shown that plants in the nursery phase can benefit, i.e. increased growth, more flowers, hardier, less transplant shock, etc., by increasing the degree of mycorrhizal development on absorbing roots. Many other plants, especially woody plants like forest trees and urban landscape trees, survive better, develop new roots faster, and are generally healthier than plants with few or no mycorrhizae in field plantings.

Commercial plant propagators can now return the missing “forest” component to their plants i.e., the “natural-state of absorbing roots”, by using commercially available inoculants of mycorrhizal fungi. These inoculants can be added to a variety of plant propagation stages to promote the development of mycorrhizae. Remember, in nature, mycorrhizal plants grow where other plants fear to grow!