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Chapter 14

Mycorrhizal Fungi and Plant Nutrition

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The term "mycorrhiza" was coined by A. B. Frank, a scientist in Germany, more than 100 years ago. It literally means fungus-root, and describes the mutualistic association existing between a group of soil fungi and higher plants. The association is based on the plant component providing carbohydrates and other essential organic compounds to the fungi. In return, the fungal component, which colonizes both the root and the adjacent soil, helps the plant take up nutrients by extending the reach of its root system.

Although mycorrhizal associations were discovered over 100 years ago, their role in plant productivity did not receive the attention it should until the past 30 years. Today, hundreds of scientists all over the world are engaged in the study of mycorrhizal associations, and any discussion of plant productivity that does not include mycorrhizal associations can hardly be considered complete.

Mycorrhizal types

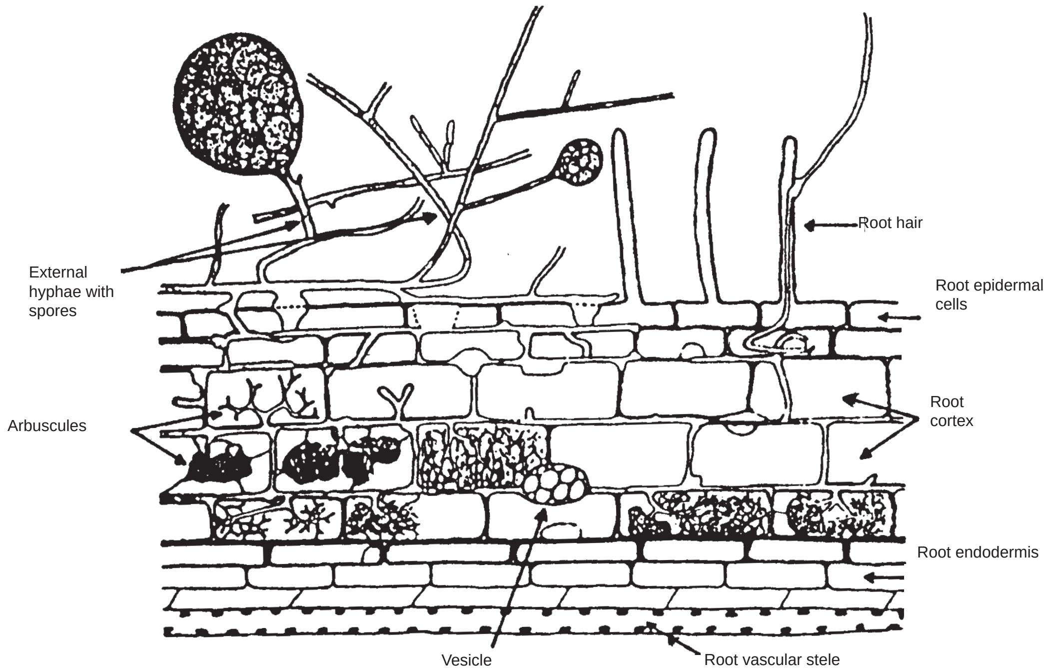
Of the many types of mycorrhizal association (see Harley and Smith 1983), two are of major economic and ecological importance: ectomycorrhizal associations, and the endomycorrhizal association of the vesicular-arbuscular (VA) type.

In ectomycorrhizal associations, the fungi invade the cortical region of the host root without penetrating cortical cells. The main diagnostic features of this type of mycorrhiza are (1) the formation within the root of a hyphal network known as the Hartig net around cortical cells and (2) a thick layer of hyphal mat on the root surface known as *sheath* or *mantle*, which covers feeder roots. Infection of host plants by ectomycorrhizal fungi often leads to changes in feeder roots that are visible to the naked eye. Feeder roots colonized by the fungi are thicker and more branched than uncolonized roots; ectomycorrhizal feeder roots also tend to be colored differently.

In endomycorrhizal associations of the VA type, the fungi penetrate the cortical cells and form clusters of finely divided hyphae known as *arbuscules* in the cortex (Figures 14-1 and 14-2). They also form vesicles, which are membrane-bound organelles of varying shapes, inside or outside the cortical cells (Figures 14-1 and 14-2). Arbuscules are believed to be the sites where materials are exchanged between the host plant and the fungi. Vesicles generally serve as storage structures, and when they are old they can serve as reproductive structures. Vesicles and arbuscules, together with large spores, constitute the diagnostic features of the VA mycorrhizas. Roots have to be cleared and stained in specific ways and examined under a microscope to see that they are colonized by VA mycorrhizal fungi. Because vesicles are not always found in these types of mycorrhizal associations, some researchers now prefer the designation arbuscular mycorrhiza (AM) over the term vesicular-arbuscular (VA) mycorrhiza.

Both AM fungi and ectomycorrhizal fungi extend hyphae from the root into the soil, and these external (or extraradical) hyphae are responsible for translocat-

Figure 14-1. Diagram of a root colonized by AM fungi showing the diagnostic features of the fungi.



ing nutrients from the soil to the root.

Most ectomycorrhizal fungi belong to several genera within the class basidiomycetes, while some belong to the zygosporic zygomycetes and ascomycetes. On the other hand, AM fungi belong to six genera within the azygosporous zygomycetes.

Host specificity

AM associations occur in a wide spectrum of tropical and temperate tree species. They are known not to occur only in a few plants, namely members of the families Amaranthaceae, Pinaceae, Betulaceae, Cruciferae, Chenopodiaceae, Cyperaceae, Juncaceae, Proteaceae, and Polygonaceae. The ectomycorrhizas, on the other hand, occur primarily in temperate forest species, although they have been reported to colonize a limited number of tropical tree species. Therefore, this chapter concentrates on AM fungi.

Functions of mycorrhizal fungi

Results of experiments suggest that AM fungi absorb N, P, K, Ca, S, Cu, and Zn from the soil and translocate them to associated plants (Tinker and Gildon 1983). However, the most prominent and consistent nutritional effect of AM fungi is in the improved uptake of immobile nutrients, particularly P, Cu, and Zn (Pacovsky 1986, Manjunath and Habte 1988). The fungi enhance immobile nutrient uptake by increasing the absorptive surfaces of the root.

The supply of immobile nutrients to roots is largely determined by the rate of diffusion. In soils not adequately supplied with nutrients, uptake of nutrients by plants far exceeds the rate at which the nutrients diffuse into the root zone, resulting in a zone around the roots depleted of the nutrients. Mycorrhizal fungi help overcome this problem by extending their external hyphae to areas of soil beyond the depletion zone, thereby ex-

Figure 14-2. A microscopic view of a root segment specifically stained to show the arbuscules and vesicles of AM fungi.

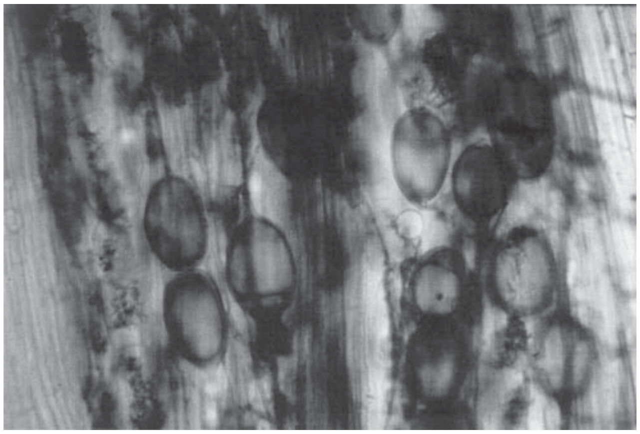
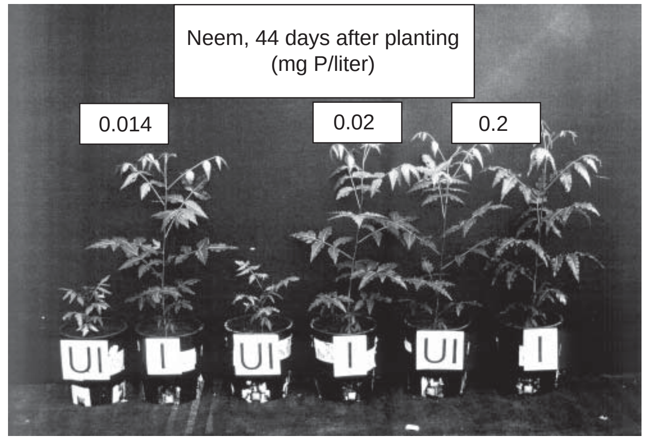


Figure 14-3. Response of neem (*Azadirachta indica*) to inoculation with AM fungus. I = inoculated; UI = uninoculated (Habte et al., 1993, *Arid Soil Res. Rehab.*)



ploring a greater volume of the soil than is accessible to the unaided root. Enhanced nutrient uptake by AM fungi is often associated with dramatic increase in dry matter yield, typically amounting to several-fold increases for plant species having high dependency on mycorrhiza (Figures 14-3, 14-4, and 14-5).

AM fungi may have biochemical capabilities for increasing the supply of available P and other immobile nutrients. These capabilities may involve increases in root phosphatase activity, excretion of chelating agents, and rhizosphere acidification. However, these mechanisms do not appear to explain the very pronounced effect the fungi have on plant growth (Habte and Fox 1993).

AM fungi are often implicated in functions which may or may not be related to enhanced nutrient uptake. For example, they have been associated with enhanced chlorophyll levels in leaves and improved plant tolerance of diseases, parasites, water stress, salinity, and heavy metal toxicity (see Bethlenfalvay 1992). Moreover, there is increasing evidence that hyphal networks of AM fungi contribute significantly to the development of soil aggregates, and hence to soil conservation (Miller and Jastrow 1992).

Application of AM Technology

Keys to successful application of AM technology are the availability of good quality inocula and a clear understanding of the circumstances under which mycorrhizal fungi are likely to enhance plant growth and development. AM fungi are obligate symbionts and therefore cannot be multiplied on laboratory media apart from a living host.

In the most common way of producing AM inocula, the fungi are multiplied in the presence of a suitable host plant growing in some kind of matrix, which may be sand, soil, or sand-soil mixture. The supply of P and other nutrients is carefully monitored to promote maximum fungal infection and spore development. This

Figure 14-4. Papaya grown in fumigated soil (UI) grows poorly without mycorrrhizal inoculation (I); a phosphorus level that is adequate when AM fungus is present is inadequate to support growth of papaya plants that lack the symbiotic association.

Figure 14-5. Response of *Leucaena leucocephala* to mycorrhizal inoculation of a fumigated field at three soil pH levels (adapted from Huang 1987).

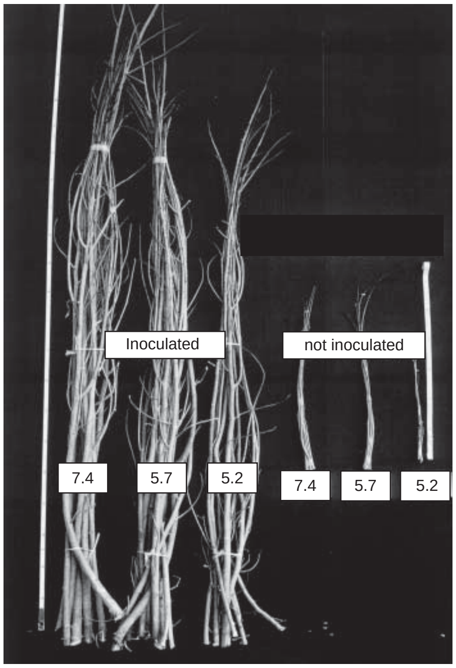


Table 14-1. VAMF dependency of selected food and tree crops.

Marginally dependent
Ananas comosus
Casssia reticulata
glycine max
lycopersium esculentum
Sesbania formosa
Sesabnia pachycarpa
Sesbania sesban
Zea mays

Moderately dependent
Acacia koa
Gliricidia sepium
Leucaena retusa
Sesbania grandiflora

Highly dependent
Acacia mangium
Albizia feruginen
Azadiarachta indica
Cajanus cajan
Cassia leschenaultania
Cassia spectabilis
Cassia siamea
Entrolobium cyclocarpa
Leucaena diversifolia
Leucaena trichodes
Paraserianthes falcatara
Sauropus androgynus

Very highly dependent
Leucaena leucocephala
Manihot esculanta
Sophora chrysophylla

process requires as long as 16–18 weeks. After this period, the medium is allowed to dry down to 5% moisture content or less. The plant is then cut off, and the remaining medium containing spores, pieces of fungal hyphae, and segments of infected roots serves as the crude inoculum. Such an inoculum can be stored at 22°C for as long as three years without significant loss in viability.

Infected roots *per se* can be exclusively used as inoculum. They can be produced in two-thirds of the time required to produce crude inocula and grown in the absence of solid media by aeroponic or hydroponic methods. However, a major problem with root inocula is their tendency to lose viability rapidly in storage, particularly at room temperature.

Until inoculum production procedures based on plant-free microbiological media are developed, direct application of AM fungi to extensive areas of land will be both cumbersome and expensive. The inoculant technology, however, is readily applicable to trees, vegetable crops, and other species that are normally transplanted. Thousands of mycorrhizal transplants can be cost-effectively produced in containers or nursery plots for subsequent outplanting to large areas of land.

The need to inoculate

The widespread occurrence of AM fungi in soils throughout tropical and temperate regions has sometimes led to the notion that inoculation of soils with AM fungi is not essential. However, inoculation is necessary where the fungi have been eliminated or their populations reduced by pesticide application, fumigation, erosion, or other forms of soil disturbance. Furthermore, undisturbed soils could have inherently low levels of AM fungi, particularly after nonmycorrhizal species have been grown on them. In some instances, indigenous AM fungi may either express their symbiotic effectiveness after a prolonged lag phase, or their inherent effectiveness may be too low, and thus they will need to be preempted by more aggressive, highly effective AM inocula (Habte and Fox 1989).

AM fungi play crucial roles in both natural and agricultural situations, including:

- native ecosystems such as forests where fertilization of extensive land areas with large quantities of P is not practical
- agricultural systems in which the high P-fixing capacities of soils and the unavailability or high cost of P fertilizer limits crop production

- situations in which it is essential to reduce soil fertilizer application rates significantly because of environmental concerns
- situations in which phosphate rock is readily available and used instead of superphosphate.

AM fungi usually have their maximum effect on host plant growth when the level of P in the soil solution is such that P is either barely accessible or inaccessible to the nonmycorrhizal plant. Because the effect of mycorrhizal colonization on host plants usually can be duplicated by P amendment of the soil, it is possible to establish categories of mycorrhizal dependency of host plants by assessing their response to AM fungal colonization at different concentrations of soil solution P (Habte and Manjunath 1991). When the soil solution P concentration is at or near 0.002 mg/liter, most plant species will respond dramatically to mycorrhizal colonization. As P concentration is increased from this level to 0.02 mg/liter, the dependency of plants on AM fungi for P uptake diminishes progressively, and at 0.2 mg/liter only the very highly mycorrhiza-dependent species respond significantly to mycorrhizal colonization. Based on this approach, we proposed five mycorrhizal dependency categories (Habte and Manjunath 1991). Table 14-1 shows plant species whose mycorrhizal dependency categories have been determined to date. Given the soil solution P concentration, the abundance and effectiveness of the native AM fungi, and the mycorrhizal dependency of the host, it is possible to predict the outcome of AM colonization of the plant.

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