Review

Mycorrhizal symbioses and plant health*

John F. Brown, Department of Botany, University of New England,
Armidale, N.S.W. 2351, Australia.

Introduction

Mycorrhizas are symbiotic associations between fungi and plant roots. They are initiated when a plant root becomes infected with an appropriate fungus. The term mycorrhiza, which means fungal root, was introduced by Frank in 1885. However, the presence of fungal hyphae in the roots of plants was recognized and described well before this time (Reissek 1847).

It is now known that mycorrhizas are essential for the establishment and growth of some plant species (e.g., orchids). In other plants (e.g., members of the family Pinaceae) growth can occur in the absence of the fungus but is better in mycorrhizal plants, particularly in soils that are deficient in immobile elements such as phosphorus and zinc.

Mycorrhizas are common in some mosses, lycopods and ferns as well as in most gymnosperms and angiosperms. Trappe (1977) estimated that about 95% of the world's present species of vascular plants belong to families that are characteristically mycorrhizal. Harley and Harley (1986) concluded that over 70% of the British flora can become mycorrhizal.

Samuel (1926) recognized ectomycorrhizas in species of eucalypt and suggested that "the roots of many, if not all, *Eucalyptus* species may possess mycorrhizas". Chilvers and Prior (1965) surveyed 152 species of eucalypts in New South Wales and the Australian Capital Territory. All were found to be mycorrhizal, although sometimes individual plants were not infected. It would seem therefore that mycorrhizal plants are the rule and not the exception.

Some plant families, particularly those that have finely divided roots with many long root hairs, rarely produce mycorrhizas. These include the families Cyperaceae, Juncaceae, Cruciferae, Chenopodiaceae and Proteaceae. Moreover, in some plant families that are characteristically mycorrhizal (e.g., Fabaceae = legumes) there are some species that do not form extensive mycorrhizas (e.g., *Lupinus* spp. = lupins).

The fungi that form mycorrhizas vary according to the type of mycorrhiza produced. Most of the major groups of fungi (Zygomycetes, Ascomycetes, Basidiomycetes and Deuteromycetes) have members which form mycorrhizas in association with various plant species.

In most mycorrhizas the fungus obtains carbohydrate that has been produced by the plant as a result of photosynthesis. Orchid mycorrhizas are unique in that the plant obtains carbohydrate from the fungus. It is likely that the fungus also obtains amino acids, vitamins and other nutrients from the plant. The plant also provides the fungus with a habitat that is free from competition from soil saprophytes, antagonists and predators.

The question that now arises is, how does the plant benefit from becoming mycorrhizal? It would seem that the hyphae of mycorrhizal fungi grow out from the infected root into the surrounding soil and act as an extension of the plant's root system. The fungal mycelium absorbs nutrients such as phosphorus and zinc as well as water from the soil and translocates these back to the plant root. Mycorrhizal plants therefore can explore and exploit a much greater volume of soil than non-mycorrhizal roots (Figure 1). This results in mycorrhizal plants having greater access to nutrients and water, particularly in infertile soils. Sanders and Tinker (1973) showed that the inflow of phosphorus into onion roots infected with a vesicular-arbuscular mycorrhizal fungus was 3–4 times more than that of uninfected roots. The influence of mycorrhizas on the mineral nutrition of plants has been discussed by Stribley (1987).

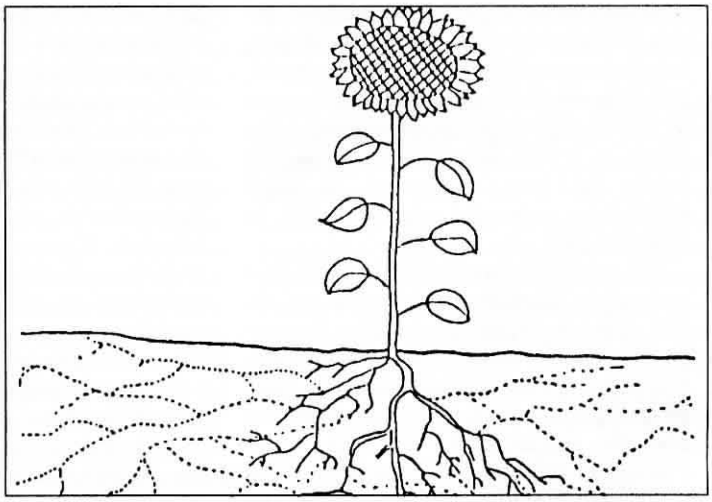

Figure 1. Diagrammatic representation of how the fungal hyphae that originate from a mycorrhizal root radiate out into the soil (broken lines represent the fungal hyphae). This enables the mycorrhizal plant to explore and exploit a much greater volume of soil than a non-mycorrhizal plant.

In their natural environment, mycorrhizal plants are normally healthier and grow more vigorously than non-mycorrhizal plants. Daft and Nicolson (1966) reported a 4.5 times greater dry weight in tomato plants infected with a vesicular-arbuscular mycorrhizal fungus than in uninoculated control plants when grown in a soil deficient in phosphorus. This difference decreased as phosphorus levels increased. They also showed that 91% of the roots became infected in inoculated plants grown in the phosphorus deficient soil compared with only 64% in the phosphorus rich soil. It would seem therefore that the extent of mycorrhizal development is inversely related to the phosphorus levels in the soil.

It has been shown that populations of mycorrhizal fungi in soil decrease rapidly after soil disturbance such as that associated with mining operations and cultivation.

The successful re-establishment of pine trees on acid coal spoils in Kentucky and Virginia in the U.S.A. has been shown to be dependent on the plants becoming infected with an appropriate ectomycorrhizal fungus. Marx and Artman (1979) found that survival and growth of loblolly pine seedlings (*Pinus taeda* L.) on these

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Footnote:

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sites was markedly increased by inoculating plants with the puffball-like fungus *Pisolithus tinctorius* (Pers.) Coker and Couch. Commercial inoculum of this fungus (MycoRhiz®) has been produced and used to inoculate container-grown ectomycorrhizal tree species before they are grown in the field (Marx *et al.* 1982).

In agricultural soils some of the so-called 'long fallow disorders', which occur in a number of crop species, are now thought to be caused by failure of inoculum of vesicular-arbuscular mycorrhizal fungi to survive during the fallow period. As a consequence, the crop that follows the fallow fails to become mycorrhizal and shows symptoms of nutritional deficiencies (Thompson 1987, Brown, Allen and Constable 1990). Thus, we have a situation where a disease occurs if the plant does not become infected by a fungus.

Other attributes of mycorrhizas include improved water uptake by plants (Safir, Boyer and Gerdemann 1971, Levy and Krikun 1980) reduced transplant injury (Mosse and Hayman 1971, Menge, Davis, Johnson and Zentmeyer 1978), improved ability to withstand high temperatures (Marx and Bryan 1971) and a reduction in the effects of pathogenic root-infecting fungi (Marx 1973, Schenck 1981, Thompson and Wildermuth 1989).

Many legumes and woody plants are simultaneously infected with nitrogen fixing bacteria (*Rhizobium* sp. in the case of legumes and *Frankia* sp. in the case of woody plants such as *Casuarina* spp.) and mycorrhizal fungi. Mosse, Powell and Hayman (1976) showed that in pot experiments, vesicular-arbuscular mycorrhizas greatly increased the amount of nodulation in *Stylosanthes* sp. It has also been shown that legumes infected with both rhizobia and vesicular-arbuscular fungi have much higher rates of photosynthesis (e.g., 52% increase in carbon assimilation; Harris, Pacovsky and Paul 1985) than uninfected controls. Chatarpaul, Chakravarty and Subramaniam (1989) showed that in the alder tree (*Alnus incana* (L.) Moench) a positive interaction occurred between infection with an ectomycorrhizal fungus (*Paxillus involutus* Batsch. ex Fr.) an endomycorrhizal fungus (*Glomus fasciculatus* (Thaxter) Gerd.) and the symbiotic nitrogen fixing bacterium *Frankia* sp. Plant growth was greatest when the plants were infected by all three organisms. It has also been suggested that nitrogen fixed within a legume might be transferred to neighbouring grasses and other non-legumes by the mycelium of vesicular-arbuscular mycorrhizal fungi should the same fungal colony infect both species (Haystead, Malajczuk and Grove 1988). Previous work using radioactive tracers showed that carbon and phosphorus can move from plant to plant along hyphal bridges (Hirrel and Gerdemann 1979, Whittingham and Read 1982, Ritz and Newman 1984). Stribley (1987) suggested that this could have important consequences for plant communities since young seedlings may become rapidly infected from an existing root network and would receive an immediate supply of phosphorus which would improve the chance of establishment by the seedling.

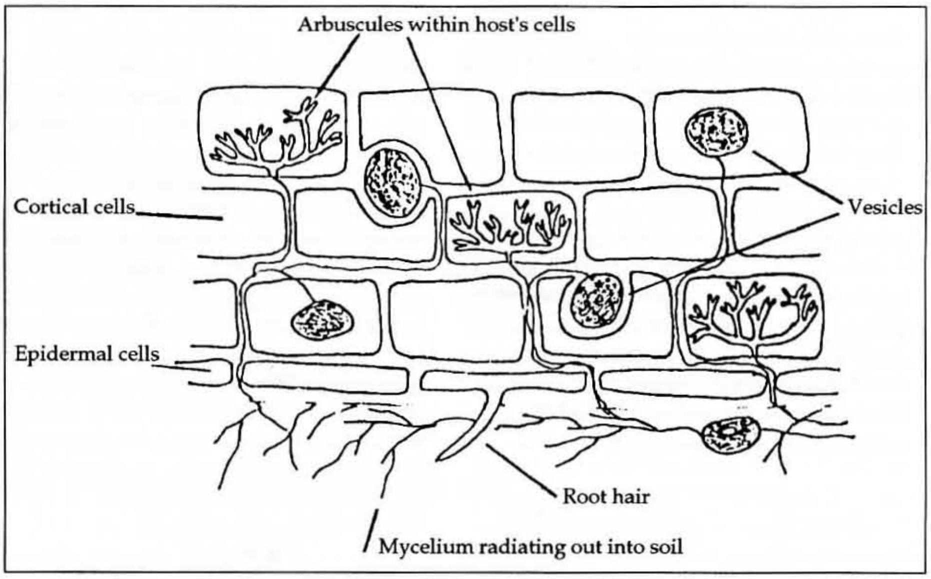

Figure 2. Diagram of a root section showing the features of vesicular arbuscular mycorrhizas.

There are a few reports of unusual circumstances when mycorrhizas may be deleterious to plant growth. One theoretical example cited by Harley and Smith (1983) was when plants were exposed to low light intensities and short days. Under these conditions rates of photosynthesis are low and the amount of carbon produced by the plant may be insufficient to compensate for the increased respiration in the infected roots and the export of carbon to the extramatrical hyphae and fruiting bodies (e.g., vesicles and spores) in the soil. Reports of detrimental effects of mycorrhizas are rare.

Types of Mycorrhizas

Frank (1887) recognized two types of mycorrhizas which he called ectotrophic and endotrophic mycorrhizas. Peyronel, Fassi, Fontana and Trappe (1969) introduced the terms *ectomycorrhiza* (a mycorrhiza where the fungus develops only on the outside of the root cells as a sheath and as a Hartig net), *endomycorrhiza* (where the fungus penetrates and grows within the root cells and does not form an external Hartig net) and *ectendomycorrhiza* (where the fungus forms a Hartig net outside the root cells but also penetrates and grows within the root cells). Nowadays several different types of mycorrhizas are recognized within these three categories.

Ectomycorrhizas (sheathing mycorrhizas)

In ectomycorrhizas the fungus forms a sheath of pseudoparenchyma around the root (usually 20–40 µm thick) with fungal hyphae growing between the outer cells of the root to produce the so-called Hartig net. The fungus does not penetrate the host's cells. The fungi involved are usually Basidiomycetes (e.g., species of *Amanita, Pisolithus, Rhizopogon, Suillus, Thelephora* and stinkhorns) and less often Ascomycetes (e.g., truffles), Zygomycetes (e.g., *Endogone* sp.) and Imperfect fungi (e.g., *Cenococcum* sp.). Many gymnosperms (e.g., members of the family Pinaceae) and angiosperms (e.g., eucalypts, oak, beech, birch and pecan) form ectomycorrhizas. Ectomycorrhizas differ in morphology from uninfected roots in that they are visibly swollen and branch either racemously (e.g., eucalypts) or dichotomously (e.g., *Pinus* spp.). Probably about 3 to 5% of the total number of plant species form ectomycorrhizas.

Vesicular-arbuscular mycorrhizas

Vesicular-arbuscular mycorrhizas or VAMs as they are commonly called are the most common and widespread type of mycorrhiza. They probably occur in about 65% of plant species including mosses, lycopods, ferns, gymnosperms and most angiosperms. VAMs occur in almost all plant families including many important agricultural species such as cereals and grasses, legumes, citrus, coffee, cotton, oilpalms, rubber, sunflower and tea. The fungi that form VAMs are thought to be Zygomycetes belonging to the newly erected order Glomales (Morton and Benny 1990) which contains those fungi that form arbuscules in root cells (Figure 2). Six genera are currently recognized; *Acaulospora, Entrophospora, Gigaspora, Glomus, Sclerocystis* and

Scutellospora (Morton and Benny 1990). Vesicular-arbuscular mycorrhizal fungi are ecologically obligate symbionts. They cannot be grown on artificial media nor can they survive as saprophytes in soil. They are dependent on their partner (the plant) for carbon and other nutrients. As a result of this they do not survive for long periods in the absence of host plants.

The name vesicular-arbuscular mycorrhizas originated because the fungus penetrates the root's epidermal and cortical cells and produces dichotomously branched, haustoria-like structures called arbuscules (Figure 2). Each arbuscule is surrounded by the host's cell membrane. The fungus also produces characteristic vesicles in or between the root cells. However, vesicles are not always present (e.g., Gigaspora) and for this reason some workers no longer use the word vesicular and simply refer to VAMs as "arbuscular mycorrhizas" (Morton 1990a, 1990b) . The interface between arbuscules and the host's cell membrane is very extensive. This allows nutrient transfer to occur in both directions between the plant and the fungus. The life span of an arbuscule varies among species but usually ranges from 2 to 15 days (Harley and Smith 1983). After this time the arbuscule progressively collapses and disappears. The host cell can then become reinfected with another arbuscule. Some workers believe that host enzymes "dissolve" the arbuscules and that the nutrients they contain are absorbed by the host. The apical region of the root is many times more susceptible to infection than other regions. Vesicular-arbuscular mycor-rhizas differ from ectomycorrhizas in that the fungus does not produce a sheath or Hartig net nor does it induce morphological changes in infected roots. The role played by vesicular-arbuscular mycor-rhizal fungi in agriculture has been reviewed by Abbott and Robson (1982).

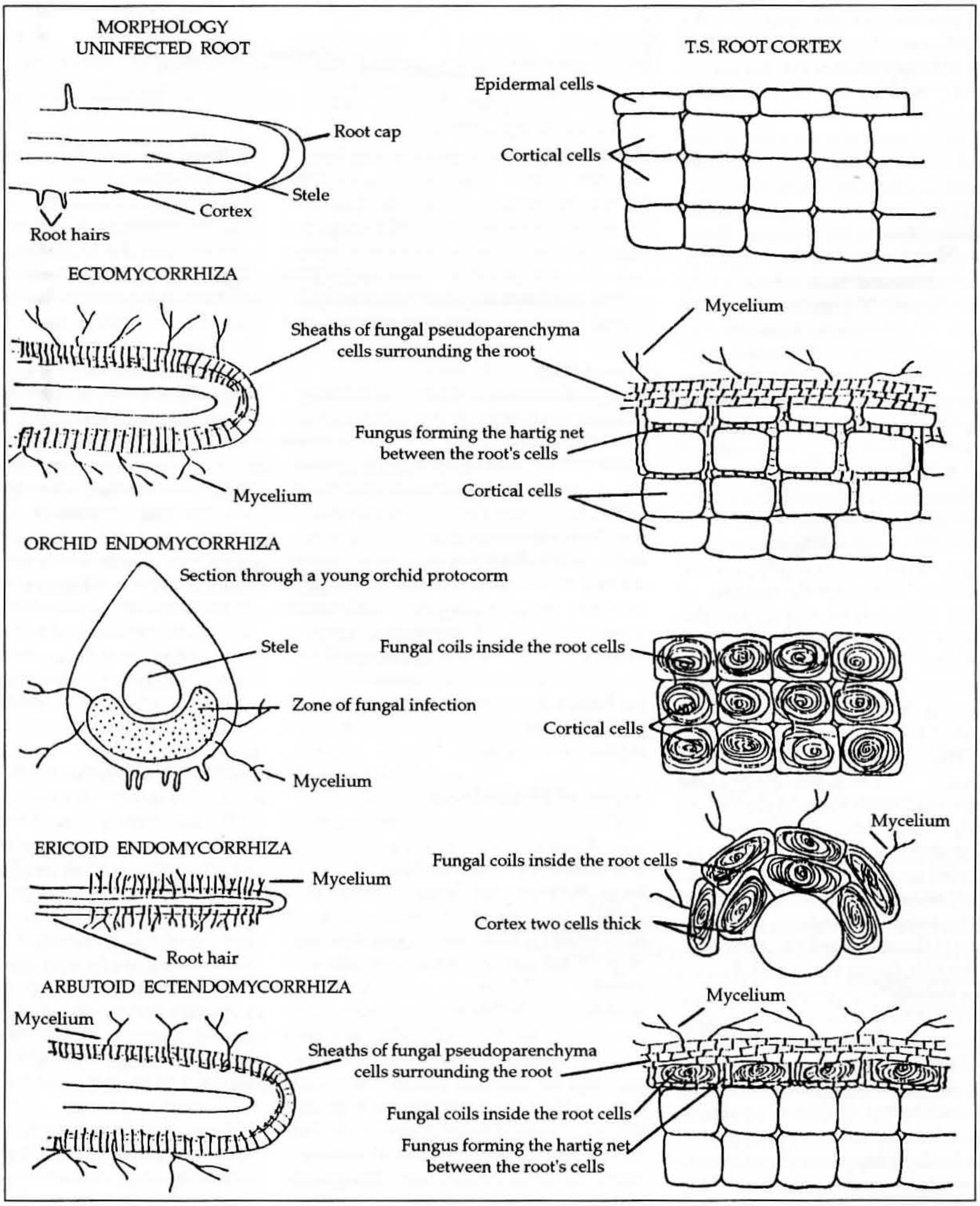

Figure 3. Morphological features of different types of mycorrhizas

Orchid endomycorrhizas

Endomycorrhizas occur in all members (over 20,000 species) of the monocot family Orchidaceae (e.g., vanilla and ornamental orchids). The fungi involved are Basidiomycetes belonging to genera such as *Thanatephorus* (including *T. cucumeris* (Grank) Donk = *Rhizoctonia solani* Kühn), *Fomes* and *Armillaria*. Many of these fungi are pathogenic on a wide variety of other plants. The fungus produces coils (often called pelotons) in the cortical cells of the root. No sheath or Hartig net is formed. In their natural environment, orchids cannot develop in the absence of their fungal symbiont. It would seem that the fungus can hydrolyse complex carbohydrates in living plant tissue or plant remains in the soil and translocate carbon compounds to the plant. Orchid seedlings are not photosynthetic and are heterotrophic for carbon.

Ericoid endomycorrhizas

Endomycorrhizas occur in members of the plant order Ericales that have a fine root system (e.g., *Azalea* spp., *Rhododendron* spp., heather, cranberry and blueberry). The fungi involved are usually slow growing, darkly pigmented and fail to sporulate readily in culture. As a consequence they are difficult to identify. One Ascomycete (Discomycete) has been identified as *Pezizella* sp. In ericoid mycorrhizas the fungus produces a hyphal mass in the cortical cells of the root system which may make-up about 42% of the total volume of the root (Read and Stribley 1973). No sheath or Hartig net is formed.

Arbutoid ectendomycorrhizas

Arbutoid ectendomycorrhizas are formed in members of the family Ericaceae that have a sturdy root system (e.g., species of *Arbutus* and *Arctostaphylos*). The fungi involved appear to be the same as those that form ectomycorrhizas with other plants (e.g., species of *Amanita, Cortinarius, Pisolithus* and *Suillus)*. The structure has characteristics of both ecto- and endomycorrhizas in that a well developed fungal sheath surrounds the root and a Hartig net is formed between the outer cortical cells. In addition, the fungus penetrates the cortical cells to produce coils.

Monotropoid ectendomycorrhizas

Monotropoid ectendomycorrhizas are found in members of the family Monotropaceae which are achlorophyllous (non-photosynthetic) members of the order Ericales (e.g., *Monotropa* spp.). The fungi involved are mostly Basidiomycetes which also form ectomycorrhizas with surrounding plants such as beech and pine trees. The fungus produces a well developed sheath and Hartig net. In addition the fungus forms peg-like, unbranched haustoria in the epidermal cells of the root.

The different types of mycorrhizas discussed are illustrated diagrammatically in Figure 3.

Summary and conclusions

Mycorrhizas are symbiotic associations between fungi and the roots of plants. They are initiated when a plant root becomes infected with an appropriate fungus. Mycorrhizas are essential for the establishment and growth of some plant species (e.g., all orchids and pine trees on disturbed sites). In other plants (e.g., cereals, cotton, sunflower) growth can occur in the absence of the fungus but is usually better in mycorrhizal plants, particularly in infertile soils. Over 90% of the world's present species of vascular plants are thought to belong to families that are characteristically mycorrhizal. A few plant families rarely form mycorrhizas.

Mycorrhizal plants appear to have several advantages over non-mycorrhizal plants. Mycorrhizal plants grow better in infertile soil because they are able to exploit a greater volume of soil which increases uptake of immobile nutrients such as phosphorus and zinc. Other advantages attributed to mycorrhizas include improved water uptake by plants, reduced transplant damage, greater ability of plants to withstand high temperatures, a reduction in the effects of pathogenic root-infecting fungi, an increase in the amount of nodulation in legumes and a subsequent increase in their photosynthetic rates, interacting with symbiotic nitrogen fixing bacteria in woody plants (e.g., Alder trees) to increase plant growth, and possibly enabling nitrogen fixed by legumes and other plants to be transferred to neighbouring non-legumes.

It is likely that in the near future, methods will be developed to manipulate and manage the amount and quality of mycorrhizas that are formed by plants. In addition to improving crop yields and quality, this may enable plants to be grown in environments where they cannot be grown at present. It may result in deserts and impoverished regions being revegetated with desirable plant species. It may enable humans to undo some of the deleterious effects that their activities have had on the environment.

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