Chapter 10

B. ENDOMYCORRHIZAE

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1. INTRODUCTION

Endomycorrhizae, which have been known to man for little more than 100 years, probably existed on our planet some 300 million years ago. Fungal infections in fossilized roots from the Devonian and Carboniferous periods (Osborn, 1909; Kidston and Lang, 1921; Boullard and Lemoigne, 1971) look remarkably like some vesicular–arbuscular (VA) infections in living roots of today. Rootlets of the Palaeozoic gymnosperm genus *Cordaites*, for example, were often found to contain a fungal endophyte with vesicles and large, mainly aseptate hyphae (Osborn, 1909). Some cortical cells contained dark masses interpreted as fungal clumps and resembling arbuscules. This interpretation, however, was questioned by Cridland (1962) who did not consider the endophyte to be mycorrhizal. As in present-day VA mycorrhizal infections, the fungus occurred in the root cortex but not in the endodermis and stele, and the infected roots appeared undamaged. Some of the large fungal spores recovered from Pleistocene deposits in North America (Dowding, 1959; Srivastava, 1968) could be mistaken for present-day spores of *Endogone*, the VA mycorrhizal fungus par excellence. These ancient spores, sometimes called *Rhizophagites*, were around 50 to 80 μm in diameter and thus similar in size to the smaller of their modern relatives.

One of the earliest reports of an endomycorrhizal infection was in 1849 and concerned a septate fungus in the roots of the orchid *Neottia nidus* (see Maeda, 1954). The roots of plants in the order Ericales were observed in 1881 (Kamienski, 1881) to be invested with fungal hyphae. In the year 1885, when Frank coined the term mycorrhiza for the fungus–root organs on certain forest trees (Frank, 1885) (now called ectomycorrhiza), an endophyte which was almost certainly of the VA type was observed in the roots of sugarcane (Treub, 1885). Soon, the VA endophyte was found to form the type of mycorrhiza that is most widespread in the plant kingdom. It was identified by Schlicht in 1889 (see Butler, 1939) in 71 species of flowering plants belonging to a range of families, including the Compositae, Rosaceae and Umbelliferae. Extensive studies by Janse (1896) in Java revealed the VA fungus in 69 of the 75 plant species he examined. These

species belonged to 56 plant families comprising bryophytes and pteridophytes as well as gymnosperms and angiosperms. He considered the endophytes in these groups to be closely related to one another but distinct from the endophytes in the Ericales and Orchidaceae. Work on endomycorrhiza has progressed steadily since then, expanding rapidly during the last decade and culminating in 1974 in the first International Symposium devoted exclusively to the subject. This symposium was held at the University of Leeds, England. Converts to endomycorrhizal studies are increasing in number throughout the world, and an endomycorrhizal "publication explosion" can be anticipated during the coming decade.

Biologists have long been fascinated by examples of organisms living intimately together for mutual benefit. When such symbiotic associations involved plants and fungi, they used to attract most attention from botanists and microbiologists who were primarily interested in physiological, anatomical, taxonomic and ecological aspects. Now plant pathologists too, after overcoming their initial prejudice against fungi being able to live extensively but quite harmlessly inside plant roots, have swelled the mycorrhizal ranks. Their recognition of the importance of endomycorrhizal infections is hinted at by the photograph of "*Rhizophagus*" in strawberry roots meriting the frontispiece position in the book "Root Diseases and Soil-borne Pathogens" (Toussoun et al., 1970). The suggestion that more plant tissue is infected by *Endogone* than by any other fungal group (Gerdemann, 1968) reinforces this recognition.

The term endomycorrhiza (or endotrophic mycorrhiza) is used to distinguish this type of mycorrhiza from ectomycorrhiza (or ectotrophic mycorrhiza) because there is usually no sheath of fungal mycelium around endomycorrhizal roots as there is around ectomycorrhizal roots. This negative criterion, however, lumps together three types of endomycorrhiza which are quite different from each other. They are often called ericalean, vesicular–arbuscular (VA) and orchidaceous mycorrhizae. They differ in the groups of host plants and fungi involved and in the host–endophyte interactions. The first two types are more akin to ectomycorrhiza than to orchidaceous endomycorrhiza in some of the interactions between plant and fungus. Each of the three groups will therefore be treated separately in this review. Most space will be given to the VA type because it is by far the most widespread and economically important and is currently receiving the most attention.

There are other possibly endomycotrophic infections of roots involving sterile imperfect fungi and a few species in such genera as *Fusarium* and *Phialophora*. Some of the non-ericalean, non-orchidaceous plants with non-pathogenic septate fungi inside their roots are discussed by Harley (1969) and will not be described here.

One major difficulty with mycorrhiza, as with all biological groupings, is that the categories are not clearcut. There is, in fact, considerable overlapping. For example, in the ericalean–arbutoid type of endomycorrhiza, there is a

mycelial sheath around the roots similar to that in ectomycorrhiza. Also *Endogone*, despite being *the* VA fungus, includes the species *E. lactiflua* which forms ectomycorrhiza with *Pinus strobus* and *Pseudotsuga douglasii* (Fassi and Palenzona, 1969). Oak, a member of the traditionally ectomycorrhizal Fagaceae family, can form VA as well as ectomycorrhiza (Grand, 1969). Conversely *Photinia glabra* in the Rosaceae, a traditionally endomycorrhizal family, forms ectomycorrhiza with *Cenococcum graniforme* (Grand, 1971). Many woody plants have both ecto- and endomycorrhiza (Meyer, 1973). These include *Corylus*, *Eucalyptus*, *Juniperus*, *Liquidambar*, *Liriodendron* and *Populus*. These two types of infection usually occur on separate roots, but in some plants such as *Leptospermum* (Baylis, 1962) there can be a double infection with an ectomycorrhizal sheath enclosing a root cortex containing arbuscules of *Endogone*. In the tuberculate mycorrhiza of Douglas fir a phycomycete ensheathes the bunch of proliferated root tips, each root tip being enveloped by a basidiomycete mantle (Trappe, 1965). In plants belonging to the Leguminosae family, the roots are often doubly symbiotic with two quite distinct microorganisms, *Endogone* and *Rhizobium*.

2. ERICALEAN MYCORRHIZA

2.1. Occurrence

Most plant genera belonging to the four or five families placed in the Ericales are believed to be mycorrhizal. Since the Ericales are only one of the many orders into which flowering plants are classified — 67 are described by Lawrence (1951) — the ericalean type of endomycorrhiza is obviously of limited taxonomic extent. Nevertheless, the Ericales occur widely and often constitute the dominant vegetation in calcifuge plant communities such as occur on heaths and moorlands. These habitats are normally very deficient in plant nutrients.

2.2. The fungal endophytes

Much controversy has surrounded the identity of the fungi that form mycorrhiza in the Ericales. Two different types of septate fungi have been implicated, viz. a species of *Phoma* which grew rapidly and produced pycnidia in culture and a dark, slow-growing fungus which did not fruit in culture. The *Phoma*, named *P. radicis*, was isolated from the roots of ericaceous plants, especially species of *Calluna* and *Vaccinium*, and also from seed coats of *Calluna*. The latter was considered a valid isolation of the mycorrhizal fungus by those (Rayner and Smith, 1929) who considered that the fungus was systemic throughout the *Calluna* plant. Most observers, however, did not see a systemic infection. Indeed, the main evidence for *P. radicis* being the

mycorrhizal endophyte in the Ericales appears to be its isolation from roots of 5 ericaceous species by Ternetz (1907) and from surface-sterilized roots of *Vaccinium oxycoccus* by Rayner and Levisohn (1940). On the other hand, many workers isolated dark-grey, sterile, slow-growing, septate fungi which formed typical mycorrhizae when back-inoculated on ericaceous plants grown aseptically.

In the various attempts at isolating and identifying the mycorrhizal endophytes in the Ericales, the best results were obtained when the roots were dissected or macerated before plating out and hyphae grew out onto the agar from the intracellular fungal hyphae. Pearson and Read (1973a) used macerated roots of *Calluna vulgaris* and *Vaccinium myrtillus* and isolated slow-growing dark mycelia from most of the fungus-containing root cells that they plated out on water agar. When inoculated aseptically onto *C. vulgaris*, *V. myrtillus*, *V. macrocarpon*, *V. oxycoccus*, *Erica cinerea*, *E. tetralix* and *Rhododendron ponticum*, most of these isolates formed typical mycorrhizae. This indicated not only that the true mycorrhizal endophyte had been isolated but also that there was little host specificity. These results are similar to those of Freisleben (1936) who isolated a sterile mycelium, named *Mycelium radicis myrtilli*, from *Vaccinium myrtillus* roots and resynthesized mycorrhiza with it on various species of *Vaccinium* and also on another 15 out of 22 ericaceous species that he tested. Many isolates obtained from soil also formed mycorrhiza with *Calluna*, even those from soil with no ericaceous vegetation. It seems therefore that these fungi are also capable of infecting other plants or of living as saprophytes. For example Brook (1952) obtained from forest soil devoid of plants belonging to the Ericales a fungus that formed a typical mycorrhiza with *Pernettya macrostigma*. McNabb (1961) observed a fungus indistinguishable from the ericaceous endophyte in the roots of *Cassinia fulvida* (Compositae), *Coprosma propinqua* (Rubiaceae) and *Nothopanax colensoi* (Araliaceae). Read (Pearson and Read, 1973a) has obtained the first sexual stage in culture of a dark, slow-growing ericaceous endophyte. It is an apothecium-producing ascomycete named *Pezizella ericae*.

The fungal endophytes of other ericalean plants have been little studied. *Arbutus menziesii*, although a member of the Ericaceae, has recently been shown to form ectendomycorrhiza with the agaricaceous basidiomycete *Cortinarius zakii* (Zak, 1974). At least six other mycorrhizal fungi were associated with the roots of this species, including *Cenococcum graniforme*, an ascomycete which forms ectomycorrhiza with several tree species (Trappe, 1969), and at least three basidiomycetes with clamp connections in their hyphae. Seviour et al. (1973) believe a basidiomycete is the endophyte in the ericoid mycorrhizae of *Rhododendron* and *Erica*. They showed a serological relationship between the pelotons of the fungus in the root and the basidiocarps of a *Clavaria* sp. constantly and specifically associated with the plants.

2.3. The infection: structure, factors influencing it

The ericalean mycorrhizae are characterized by non-pathogenic penetration of the root cortex by septate fungal hyphae which often form intracellular coils (pelotons) or hyphal masses and by the development of an extensive mycelium in the soil on and around the roots. Structurally these mycorrhizae fall into two groups, termed arbutoid and ericoid. The arbutoid group comprises the Arbutae section of the Ericaceae, the Pyrolaceae and the Monotropaceae. The ericoid group consists of the rest of the Ericaceae and the Epacridaceae.

Arbutoid mycorrhizae have fairly thick roots and in *Arbutus* there are long and short roots. The former can be invaded to some extent whereas the latter are strongly invaded and often encased by a hyphal sheath. As the sheath develops the rootlets become swollen. These infected short roots of *Arbutus* are thus tuberculate and are more like the ectomycorrhizae of certain forest trees than typical endomycorrhizae. After the mantle has formed the fungus penetrates the root cortex and forms intracellular hyphal coils which are later digested. These cells can be reinvaded and the process repeated. The combination of a fungal sheath around a root and an extensive intracellular hyphal growth is often referred to as ectendomycorrhiza.

In contrast to the tuberculate arbutoid mycorrhizae, the ericoid mycorrhizae are formed in a dense system of fine roots whose thin cortex of one to three layers surrounds a narrow stele. These fine rootlets are sometimes called "hair roots". They are often surrounded by a loose weft of mycelium and many of the cortical cells are invaded by the mycorrhizal endophyte. The hyphae do not enter the stele, although they may pass from cell to cell. When the cortex is only one cell layer thick the cortical cells are usually penetrated from the external mycelium rather than by hyphae from adjacent infected cells. Digestion of the intracellular fungus may be fairly rapid, the host nucleus enlarging before the hyphal structure disintegrates (Rayner, 1927). After digestion is complete, the host nucleus resumes its normal size and the whole process can occur several times during the growing season.

The intensity of infection increases during the growing season. It is least in the spring, presumably because the roots are growing faster than the fungus then. It is also affected by nutrients. Burgeff (1961) showed an inverse relationship between nitrogen level and root infection, the roots of plants growing at low nitrogen levels being profusely branched and heavily mycorrhizal. Similarly Morrison (1957) found that mineral fertilizers added to soil decreased mycorrhizal infection in *Pernettya macrostigma*. Ammonium nitrate, sodium diphosphate and calcium phosphate all decreased the intensity of infection, although infection was increased by heavy dosages of soluble phosphate which greatly upset the balance of soil nutrients and inhibited root growth.

2.4. Host—endophyte interactions and physiology

According to Henderson (1919), plants in the Ericales form a morphological series from vigorous trees such as *Rhododendron* in the Ericaceae through the less vigorous Pyrolaceae to the achlorophyllous *Monotropa* in the Monotropaceae. This arrangement, which appears to correspond to an increased dependence on saprophytic nutrition (cf. the Orchidaceae), correlates approximately with an increased development of mycorrhiza. However, as Harley (1969) points out, any correlation-based hypothesis that saprophytic angiosperms may be obligately mycorrhizal needs experimental evidence to support it.

There are few physiological studies on host—endophyte interactions in the Ericales. Some indicate that the fungus improves growth of the host plant in nutrient-deficient soils, but such studies are rare compared to the many growth experiments with other types of mycorrhiza. Brook (1952) observed some stimulation of seedlings of *Pernettya macrostigma* growing in soil and possessing mycorrhizal infection. Conversely Morrison (1957) found mycorrhizal plants of *P. macrostigma* grew slightly slower than non-mycorrhizal ones in a range of soils except for a very nutrient-deficient soil where mycorrhizal plants were able to grow but non-mycorrhizal ones were not. The slower growth of the mycorrhizal plants may not have been an effect of mycorrhiza, however, because they were growing in unsterile soil whereas the non-mycorrhizal ones were in autoclaved soil. More recently Bannister and Norton (1974) obtained similar results with *Calluna*. They found that plants with mycorrhiza generally grew worse than plants without where nutrients were plentiful but better where nutrients were low. Since the Ericales usually grow naturally in impoverished soils, the presence of a mycorrhizal infection would therefore seem to be an ecological advantage to the host plant. Comparable experiments with arbutoid mycorrhizae are lacking but would be of considerable interest in view of their morphological similarity with ectomycorrhizae for which there is a wealth of information.

Recent studies with ericoid mycorrhizae in aseptic culture have shown that the fungus can transfer phosphate from an external source into the host plant. Pearson and Read (1973b) added labelled ^{14}C and ^{32}P compounds to the fungus separated from *Calluna vulgaris* and *Vaccinium oxycoccus* seedlings by a diffusion barrier in split plates to ensure that any transfer of nutrients was due to translocation within the hyphae and not to external diffusion. They found that ^{14}C-labelled glucose was not transported into the plant whereas ^{32}P-labelled compounds were translocated through the fungal hyphae to both the *Calluna* and *Vaccinium* seedlings. The bigger the plant, the greater was the phosphate flux. Further work is needed to determine whether phosphate is accumulated in the mycobiont as it is in beech ectomycorrhiza, for example. Mycorrhizal roots of *Calluna* also show more phosphatase activity than non-mycorrhizal roots in aseptic culture and the

fungus can utilize soluble phytate (Pearson, 1971). It is not known, however, whether ericalean mycorrhizae can use phytate in soil, the bulk of which is insoluble.

At one time the endophytes of the Ericales were suspected of being able to fix atmospheric nitrogen, but this is not now considered likely. The evidence is critically reviewed by Harley (1969). However, the endophytes may have access to organic nitrogen compounds in the soil, and better nitrogen nutrition of mycorrhizal compared to non-mycorrhizal plants may prove to be more striking than mycorrhizal effects on phosphate nutrition (Stribley and Read, 1975).

Little is known concerning the effects of the host plant on the fungus. The widespread occurrence of the infection in the Ericales shows that the fungus is provided with a good ecological niche. Nevertheless, the endophyte is not totally dependent on the plant as it can be cultured in the absence of a plant and can also be isolated from soils lacking ericaceous vegetation. The experiments of Pearson and Read (1973b) with mycorrhizal *Calluna* seedlings in aseptic culture showed a transfer of ^{14}C-labelled photosynthate from the host plant into the external mycelium of the fungus. In *Vaccinium macrocarpon* $^{14}CO_2$ moves to the endophyte where it accumulates in the specifically fungal carbohydrates mannitol and trehalose and in insoluble polymers of mannose (Stribley and Read, 1975).

The degree of parasitism of one organism upon the other changes with any decreased photosynthetic ability of the plant. An extreme example is *Monotropa* which seems to be nutritionally parasitic on a fungus. Björkman (1960) believes that *M. hypopithys* derives nutrients from another plant with which it shares a common mycorrhizal fungus. He injected ^{14}C-labelled glucose and ^{32}P-labelled inorganic phosphate into the phloem of conifers and later detected radioactivity in adjacent saprophytic plants of *M. hypopithys*. Little or no ^{32}P showed up in other nearby plant species. Björkman also synthesized mycorrhiza in pine in culture with a fungus isolated from *Monotropa* roots. Electron microscope studies on *M. uniflora* by Lutz and Sjolund (1973) showed roots enveloped by a sheath whose hyphae had dolipore septa, a basidiomycete characteristic. Fungal haustoria penetrated the epidermal cells. The epidermal cell walls formed projections in the region of fungal invasion, thereby increasing the area of host–endophyte contact and so presumably the transfer of metabolites, although this may also have been a defence reaction by the plant. Rhizomorphs linking the mantle with decaying wood may provide another source of carbon, but this needs experimental proof.

2.5. Interactions with other microorganisms

The ericalean endophytes can interact with other soil microorganisms. Handley (1963) attributed the failure of certain conifers to form normal

mycorrhizal root systems in heathland soils to a possible antagonistic effect of the *Calluna* endophyte on the ectomycorrhizal fungi of the trees. Stalder and Schultz (1957) found most *Olpidium* disease of nursery plants of *Erica gracilis* in richly fertilized plants lacking mycorrhiza and suggested that wild *Erica* plants may be free from attack by *Olpidium* because of antagonism by their mycorrhizal endophytes.

2.6. Conclusions

Generalizations about host—endophyte interactions in the Ericales are difficult because the host plants encompass such a broad nutritional range. At one end of the scale there are the green species where there is transfer of phosphate from fungus to plant as in the ecto- and VA mycorrhizae. At the other end are the saprophytic, semi-saprophytic or epiparasitic species where there may be transfer of carbon from fungus to host plant as in orchidaceous mycorrhizae. Morphologically the ericalean mycorrhizae include ecto- and endomycorrhizal types. Taxonomically, basidiomycete and ascomycete fungi are involved. There are clearly many interesting areas for further study, in particular the uptake of phosphorus and nitrogen compounds from nutrient-deficient soils and the possible use of carbon in complex humic compounds.

3. VESICULAR—ARBUSCULAR MYCORRHIZA

3.1. Occurrence: host plants and habitats

The vesicular—arbuscular (VA) fungi form mycorrhiza in far more plant species, families and orders than all the other types of endo- and ectomycorrhiza combined. Indeed Meyer (1973) estimates that most Phanerogams have endo- (almost entirely VA) mycorrhizae but only about 3% have ectomycorrhizae. Because of their prevalence VA mycorrhizae, if they affect plant growth to any extent whatsoever, are potentially extremely important both economically and ecologically. They occur in most cultivated crops and in most plant species growing in natural ecosystems. Important crops with VA mycorrhiza include wheat, maize, potatoes, beans, soybeans, tomatoes, strawberries, apples, oranges, grapes, cotton, tobacco, tea, coffee, cacao, sugarcane, sugar maple and rubber trees (see Gerdemann, 1968). Wild plants with VA mycorrhiza (see Stelz, 1968; Khan, 1974; Mejstrik, 1972; Mosse and Hayman, 1977) include trees such as ash and oak, shrubs such as hazel, climbers such as honeysuckle, and a multitude of herbaceous plants of woodland and meadow, mountain and seashore. VA mycorrhizae are especially widespread in tropical tree species (Redhead, 1968). In addition to angiosperms and gymnosperms, they are found in pteridophytes and bryophytes. Very few of the many plant families examined

do not have VA mycorrhizae (Maeda, 1954; Boullard, 1968; Gerdemann, 1968; Harley, 1969). Only the Ericales, Orchidaceae and certain ectomycorrhizal families such as the Pinaceae and Betulaceae are believed to definitely lack VA mycorrhiza, although it may be rare or absent from many species in such families as the Cruciferae, Chenopodiaceae, Caryophyllaceae, Cyperaceae and Polygonaceae. Swedes, for example, seem to be non-mycorrhizal (Hayman et al., 1975). It is widespread in the two major crop families, the Gramineae and Leguminosae.

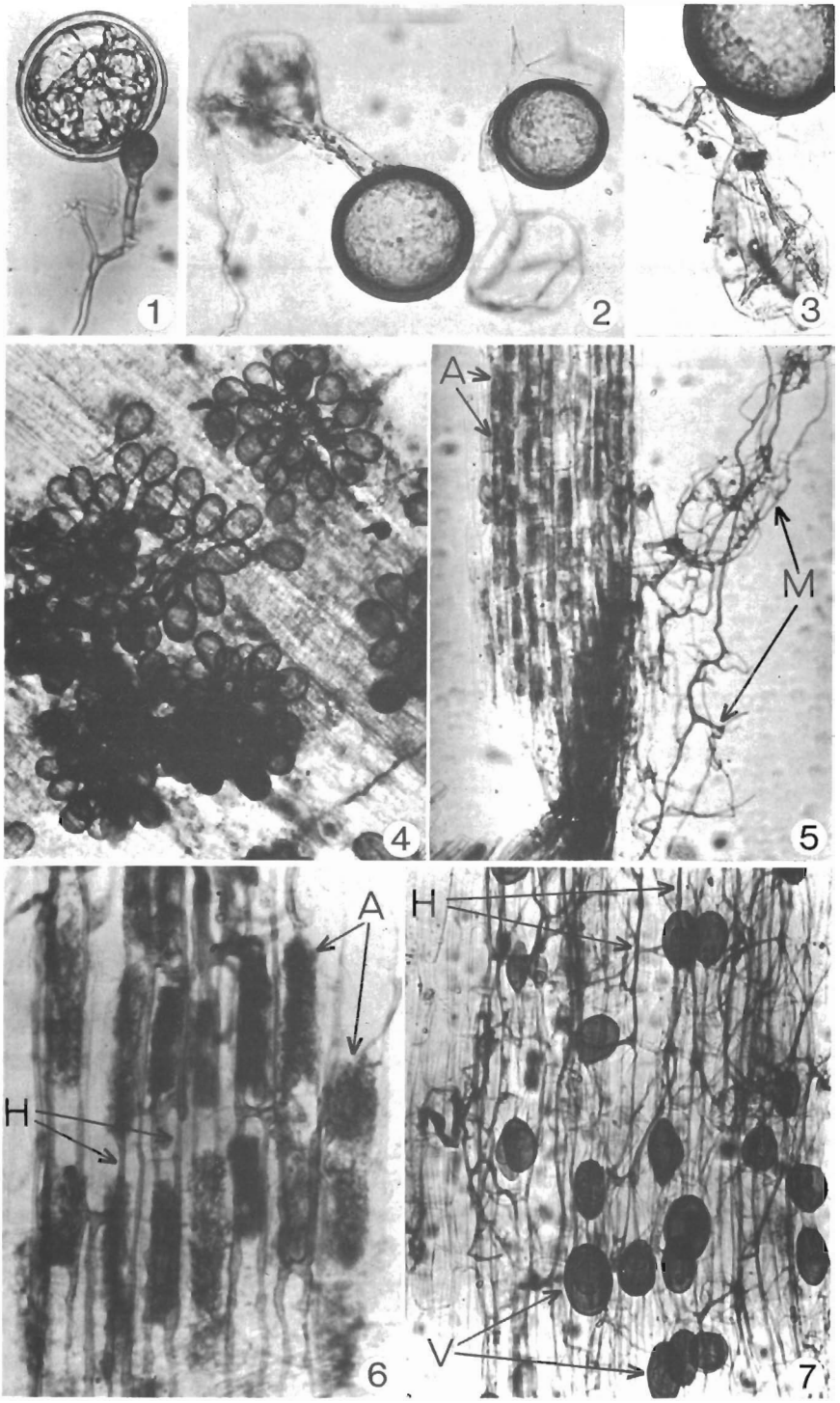
VA mycorrhizae, in addition to their widespread distribution throughout the plant kingdom, are also geographically ubiquitous and occur in plants growing in arctic, temperate and tropical regions. Their profusion in tropical forests, on an individual tree basis, is probably comparable to the abundance of ectomycorrhizae on trees in temperate forests. They also have a broad ecological range. They are generally absent only from very wet habitats, excluding salt marshes; this is especially so where the root systems are submerged as with aquatic plants and rice, although rice plants become infected in non-flooded soil. Frequently, but by no means always, plants growing in infertile soils have more VA mycorrhiza than plants growing in fertile soils. This is reflected in a generally high level of VA mycorrhiza in plants growing in uncultivated soils in contrast to its rarity in intensely cultivated garden soils. Thus man's activities, including the use of pesticides and heavy dosages of fertilizer, can decrease its extent. However, some crops such as maize are often heavily mycorrhizal, even in very fertile soils (see Hayman, 1975b). In general V A mycorrhizal infection seems more abundant in orchard and plantation crops than in annual field crops (Butler, 1939). Individual plants without mycorrhiza are probably rare in many soils.

Early work with VA mycorrhizae was not at all in proportion to their abundance and mostly dealt with their anatomy and occurrence. Until fairly recently they were virtually ignored by most soil microbiologists, soil chemists and plant physiologists. They passed unnoticed primarily because they have little effect on root morphology and because the fungal endophytes cannot be grown in pure culture. Thus, unlike ectomycorrhizae, VA mycorrhizae are not readily distinguishable from uninfected roots and, unlike the ecto-, ericalean and orchidaceous mycorrhizae, they have not been isolated from infected roots except for an *Endogone*-like fungus isolated by Barrett (1961) and plant roots where a *Pythium* species was considered to be the VA endophyte (Hawker, 1962). Also the VA fungi do not form colonies on the traditional soil dilution plates of the soil microbiologist, even though they can constitute a major proportion of the hyphae present in soil (see Warcup, 1957, and Jackson, 1965).

3.2. *The fungal endophytes*

The VA fungi were classed as phycomycetes because they lack regular septa, and VA mycorrhiza has sometimes been called phycomycetous mycorrhiza. They have usually been assigned to the genus *Endogone*, family Endogonaceae, order Mucorales. This order is currently placed in the Zygomycotina, the term "phycomycetes" now being considered taxonomically defunct. The first name given to the endophyte was *Rhizophagus populinus* by Dangeard (1900) who described a VA infection in poplar roots not as an endomycorrhiza but as a disease probably caused by a chytrid — "ses ravages dans l'écorce sont considérables"! Peyronel (1923) was the first to associate the VA infection with the genus *Endogone* by demonstrating hyphal connections between *Endogone* sporocarps and the mycorrhizal roots of certain alpine plants. The VA endophyte in garlic roots was isolated in pure culture and described as a *Pythium* which produced mycorrhiza when back-inoculated onto the host (Hawker, 1962). In almost every other instance, however, the VA fungus was an *Endogone*, as demonstrated by Peyronel (1923), Mosse (1953), and the many workers since then who have inoculated a wide range of plant genera with *Endogone* propagules to produce VA infection. The strict application of Koch's postulates to *Endogone* was not possible because of its inability to grow in pure culture, although nowadays aseptically grown seedlings can be inoculated with surface-sterilized *Endogone* spores to establish VA mycorrhiza in two-membered cultures (Mosse and Phillips, 1971). The inability of the VA endophyte to grow alone in pure culture is surprising in view of its lack of specificity in the host plants it will infect — the same isolate of *Endogone*, for example, can establish VA mycorrhiza with completely unrelated plants such as onion, strawberry, violet, sweetgum, and diverse legumes and grasses. The studies on the various possible VA fungi, culminating in the acceptance of *Endogone* as *the* VA endophyte, are comprehensively reviewed by Butler (1939), Mosse (1963), Gerdemann (1968) and Harley (1969).

Plate 1. (Facing page) *Endogone* spores and vesicular—arbuscular mycorrhizal infections.
Fig. 1. *Endogone* spore of the "bulbous reticulate" type which resembles *Gigaspora calospora*.
Figs. 2 and 3. *Endogone* spores of the "honey-coloured sessile" type which is synonymous with *Acaulospora laevis*.
Fig. 4. Small *Endogone*-like spores occurring in loose sporocarps on grass roots and connected to the infection inside the root. This type resembles the *Endogone (Glomus) fasciculata* group.
Fig. 5. Part of clover root inoculated with the "E3" spore type of *Endogone* and showing dense arbuscular infection (A) and external mycelium (M).
Fig. 6. Part of cortex of clover root inoculated with the "E3" spore type of *Endogone* and showing intracellular granular arbuscules (A) and intercellular distributive hyphae (H).
Fig. 7. Part of cortex of onion root inoculated with the "E3" spore type of *Endogone* and showing vesicles (V) and distributive hyphae (H).
Magnification = × 197 for Figs. 1,2,3,4,5, and 7, and × 500 for Fig. 6 (before reduction by 58% for page size).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The various species of *Endogone* are distinguished chiefly by the morphology of their large resting spores. These spores are generally round or oval and contain oil globules. They are the largest fungal spores known. Some are around 50 μm, many are between 100 and 200 μm and a few are nearly one mm in diameter (see Plate 1, Figs. 1—4). Their large size makes them recoverable from soil by the technique of wet-sieving and decanting (Gerdemann and Nicolson, 1963). The main ones are described by Gilmore (1968), Mosse and Bowen (1968a), Nicolson and Gerdemann (1968) and Gerdemann and Trappe (1974). In some species of *Endogone* the spores are borne in sporocarps, in others they are ectocarpic resting spores formed on the external mycelium around roots. Those species that produce large sporocarps which are often 1 or 2 cm in diameter are not known to form VA mycorrhiza, although at least one of them is said to form ectomycorrhiza. The species without sporocarps and a few of those with small sporocarps one mm or so in diameter, such as the "yellow vacuolate" spore type, are the ones principally involved in VA mycorrhiza in temperate regions.

The nomenclature of the spore types or species of *Endogone* is somewhat confusing. One of the two major systems currently in use (Mosse and Bowen, 1968a) gives the different spore types descriptive names based on distinctive morphological features. The other (Gerdemann and Trappe, 1974) gives them different generic and species names, partly according to whether they are chlamydosporic, zygosporic or azygosporic. The latter scheme includes four genera, viz. *Glomus*, *Gigaspora*, *Acaulospora* and *Sclerocystis*, which contain species forming VA mycorrhiza; the name *Endogone* is restricted, in accordance with taxonomic priorities, to those species forming sporocarps that contain true zygospores as described by Link in 1809 (Gerdemann and Trappe, 1974) and does not embrace any species known to form VA mycorrhiza. The divergence in nomenclature does not matter where a particular species can be recognized in both systems — the "yellow vacuolate" spore type of *Endogone* in the former system is *Glomus mosseae* in the latter, for example, and "honey-coloured sessile" is *Acaulospora laevis* (Plate 1, Figs. 2 and 3). Unfortunately such cross-links are not always possible, as with "white reticulate" and "bulbous vacuolate". More exchanges of spores between workers would help confirm which species and indeed genera are universally recognizable. Ultimately it is hoped that different species will be established in pure culture and specific isolates compared and their life-cycles determined to confirm species separation. At present different VA species are maintained in pot cultures with host plants growing in sterilized soil. When citing VA studies in this review I will employ the name of the fungus used by the author in question and retain the name *Endogone* when referring to the VA endophytes in general.

3.3. *The infection: structure*

The chief diagnostic feature of vesicular—arbuscular mycorrhiza is the presence of vesicles and arbuscules in the root cortex. The endodermis, stele and root meristems are not invaded. Inter- and intracellular hyphae are also present in the cortex and the infection inside the root is directly linked to an external mycelium which spreads and ramifies in the soil (Plate 1, Fig. 5). A good diagram of a generalized VA infection is presented by Nicolson (1967). The characteristic structures are well illustrated and discussed by Mosse (1963).

A VA infection usually begins with an appressorium on the root surface from which hyphae penetrate the epidermal cells. The hyphae spread inter- and intracellularly through the outer cortex where they often form coils. In the middle and inner cortex, and to a lesser extent in the outer cortex, intercellular distributive hyphae grow parallel to the root axis and lateral branches from them penetrate cortical cells to form arbuscules (Plate 1, Fig. 6). An arbuscule develops within a host cell by repeated dichotomous branching of the invading hypha to yield a cluster of fine filaments; it later breaks down to form a granular mass — the so-called digestion stage. The host nuclei become enlarged in these invaded cells. Arbuscules are structurally analogous to haustoria in the mildew and rust fungi but probably release materials to the cell in addition to absorbing nutrients within the cell. Vesicles develop inter- or intracellularly as swellings along or at the tips of the distributive hyphae (Plate 1, Fig. 7). They usually form as the infection ages, although I have found both arbuscules and vesicles in onion roots one week after inoculating them with "yellow vacuolate" *Endogone* spores and infected root fragments. The vesicles probably function as temporary storage organs. The root tips are not normally infected. Despite the density of a VA infection, there is little effect on root morphology. A bright yellow colour of the roots of some plants, e.g. onions, maize, tomatoes (which disappears on exposure to light), may be the only visible evidence of VA infection. Staining is necessary (e.g. Phillips and Hayman, 1970) to reveal the internal infection. Sometimes internal changes in root anatomy can occur as in tomato plants where VA infection can increase the amount of vascular tissue (Daft and Okusanya, 1973b).

The external mycelium forms a loose network in the soil around VA mycorrhizae. The dimorphic nature of these hyphae is highly characteristic. The main network is formed from coarse hyphae 20 to 30 μm in diameter which are thick-walled and often "knobbly" (see Nicolson, 1967). From the "knobs" arise fine hyphae 2 to 7 μm in diameter which are thin-walled and ephemeral, often penetrate particles of soil organic matter, and become septate as they die. Large resting spores are produced on the coarse external hyphae.

VA infections may be sporadic or very extensive in roots. Feeder rootlets

are more heavily infected than thicker roots, and roots which have lost their cortex are obviously uninfected. Approximately one third of the length of feeder rootlet can be infected in woodland plants (Mosse and Hayman, 1977); in cultivated plants infection may be more than one third, as in maize and grapevine (Hayman et al., 1976) and some legumes and vegetables (Sutton, 1973), but less than one third may be more common in other crops such as wheat, barley and potato (Hayman, 1975b).

3.4. The infection: factors influencing it

The intensity of a VA infection is affected by various factors, including fertilizers and plant nutrition, pesticides, light intensity, season, soil moisture, pH, inoculum density and plant susceptibility. At individual sites additions of phosphate and nitrogen fertilizers are often associated with a decrease in VA infection, as occurs in ecto- and ericalean mycorrhizae. However, no widespread generalizations can be made for field conditions because of conflicting results at some localities, probably due largely to the initial fertility of the soil (see Hayman, 1975b), and because of the lack of an inverse correlation between VA infection and soil fertility when several localities were compared (Hayman et al., 1976). Pot experiments in the glasshouse indicate a generally negative effect of P and N on infection. With additions of soluble phosphate the increased concentration of P in the plant tissues seems to be the main factor restricting spread of the endophyte (Mosse, 1973b). Pesticides, including formalin (Hayman, 1970), methyl bromide and chloropicrin (Kleinschmidt and Gerdemann, 1972), and various fungitoxicants (Nesheim and Linn, 1969) decrease VA mycorrhiza in the field. By contrast, field applications of certain nematicides can increase VA mycorrhizal infection in cotton roots (Bird et al., 1974). Jalali and Domsch (1975) decreased VA infection by coating wheat seeds with systemic fungicides such as benomyl. This could perhaps be developed into a useful technique to provide non-mycorrhizal control plants and hence more "natural" growth experiments using unsterile soil, because the experimental soils have usually had to be sterilized to eliminate the indigenous *Endogone* population. Decreased light can have a negative effect on VA infection. This topic has been discussed and further evidence presented by Hayman (1974) who found shading or decreasing the daylength reduced arbuscular development and infection density more than the actual length of root infected.

Seasonal effects have been recorded in the field, VA infection increasing during the growing season (Mason, 1964; Hayman, 1970). This is to be expected when root growth is slower in late summer than during the spring because continued growth of the fungus throughout the summer will then inevitably lead to an increase in per cent root infection. A similar explanation could account for the higher per cent infection in soils given little compared to medium or much phosphate (Hayman et al., 1975) by root

growth but not fungal growth being retarded by inadequate phosphate nutrition. Thus some reports of high per cent infection in infertile soils may be largely influenced by limited root growth and there may be more total infection in fertile soils where a lower per cent root length infected may be more than balanced by extra overall root growth.

Sutton (1973) noted a three-phase pattern of mycorrhizal development in several crops grown in field plots and in controlled environments. The initial lag phase of 20 to 25 days was attributed to rapid root growth of the seedlings and the time taken for spore germination, germ-tube growth and penetration of the host by *Endogone*. The second phase, lasting 30 to 35 days, during which there was extensive mycorrhizal development, coincided with most shoot growth and the development of much external *Endogone* mycelium leading to multiple infections. The third phase, when the proportion of mycorrhizal to non-mycorrhizal roots remained constant, corresponded approximately with host fruiting and continued until host senescence. Thus endomycorrhizae were probably well established during the grand period of growth when most nutrient uptake is believed to occur.

3.5. Resting spores: production and distribution

Spore numbers can be expected to be related to the amount of root infection in general when they are formed on the mycelium around infected roots, except where toxic factors inhibit the development of external mycelium or root growth is much restricted by poor nutrient supply. Thus in a well cultivated clay loam both infection and spore numbers were similarly affected by N fertilizer (Hayman, 1970). More spores are likely to occur at intermediate than at low levels of phosphate if lack of phosphate restricts growth enough to affect the total, but not per cent, root infection (see Khan, 1972; Hayman et al., 1975). Spore formation is generally associated with a slowing down or cessation of root growth and this can account for spore populations reaching their maxima earlier in the season than the level of VA infection (see Hayman, 1970). In pot studies, Daft and Nicolson (1972) found spore numbers and infection levels in maize were closely related, but the size of a mycorrhizal plant was related more to the numbers of spores formed around its roots than to the per cent, but not total, root infection. In uncultivated soils the occurrence of low spore numbers despite high root infections (see Mosse and Bowen, 1968b) is probably due to the low spore-producing ability of the indigenous endophytes (see Baylis, 1969). Thus wild plants may be more heavily mycorrhizal than cultivated plants, yet the resting spores of the VA endophytes are more abundant in cultivated soils, particularly those growing annual crops, than in uncultivated natural ecosystems. The low production of spores in woodlands and grasslands may be due to spores being less necessary for survival where the endophyte can overwinter in living roots compared to cultivated soils where survival struc-

tures (i.e. spores) are necessary for the fungus to persist between crops. It seems more likely that species able to form many resting spores have been selected from a mixed population in soils growing annual crops than that the same species produce many more spores in cropped than in undisturbed soil. This could be tested experimentally. Spore numbers in the field are also affected by the previous cropping history of the soil (see Kruckelmann, 1973) and by soil type (see Khan, 1971; Kruckelmann, 1973). Most spore types are widely distributed around the world (see Mosse, 1973a). Some spore types are more sensitive to certain soil treatments than others, so that a population of *Endogone* spores can be affected qualitatively as well as quantitatively. For example numbers of "white reticulate" spores were decreased relatively more than numbers of "bulbous reticulate" and "laminate" spores in a sandy wheatfield soil given nitrogen fertilizer (Hayman, 1975b). Usually qualitative differences in spore populations in cultivated soils cannot yet be explained, as in the two adjacent fields at Rothamsted with the same crop, soil type, climate and so on but where one field has only "laminate" spores whereas the other contains four spore types (see Hayman, 1970).

3.6. Host—endophyte interactions and physiology

Much of the current interest in VA mycorrhiza centres on the effects of the fungal endophyte on growth of the host plant. Indeed 37 papers published from 1968 to 1973 dealt with this topic (Mosse, 1973a). Most work has been concerned with phosphate nutrition because P is a major plant nutrient and in soils deficient in readily soluble phosphate infection with *Endogone* can stimulate plant growth by several hundred per cent. This stimulation of plant growth can occur in a wide range of soils (Hayman and Mosse, 1971) and with many plant species (Gerdemann, 1968; Mosse, 1973a). Table I gives some examples. Sterilized soils are normally used for such growth experiments because most unsterilized soils contain *Endogone* propagules; the problems this creates and the methods of inoculation are comprehensively discussed by Gerdemann (1968) and Mosse (1973a). It is a striking fact that, in the many growth experiments with VA mycorrhiza carried out by several investigators in various countries in conditions where there was insufficient phosphate in the soil for adequate plant growth, it has become almost commonplace to measure much more P taken up by plants that are mycorrhizal than by plants that are not. This is highly significant in view of the fact that most soils not given fertilizer are low in plant-available phosphate, the average orthophosphate concentration of around 10^{-6} *M* (0.03 ppm P) or less in the soil solution of unamended soils being near the limit at which many plants can take up adequate phosphate for growth.

The experiments recording improved P uptake by plants when they are mycorrhizal have stimulated recent attempts to locate the mechanism or

TABLE I

Growth responses of different plant species to vesicular—arbuscular mycorrhiza in soils containing various amounts of available (labile) phosphorus

Note: (1) Available soil P was estimated in 0.5 *M* $NaHCO_3$ extracts in the first four references and in dilute acid extracts in the last three.
(2) At low levels of available soil P, plants generally responded greatly to vesicular—arbuscular mycorrhiza; at high levels of available soil P, plants usually grew well irrespective of whether they were mycorrhizal.
(3) The level of available soil P at which a plant responds to mycorrhiza differs for different plant species.

Plant species	Site of soil collection	ppm available P	Plant dry weight (g)		Length of expt. (weeks)	Reference
			Mycorrhizal	Non-mycorrhizal		
Coprosma robusta[a]	Decid. copse	188	1.90	2.10	26	Hayman and Mosse (1971)
Coprosma robusta[a]	Arable fallow	12	1.50	0.10	26	
Allium cepa	Forest nursery	47	0.48	0.42	10	Hayman and Mosse (1972a)
Allium cepa	Arable fallow	26	0.47	0.36	10	
Allium cepa	Grassy common	18	0.65	0.07	10	
Allium cepa	Wheatfield	16	0.64	0.03	10	
Allium cepa	Decid. forest	10	0.23	0.17	10	
Allium cepa	Heath	8	0.16	0.01	10	
Allium cepa	Heath	5	0.12	0.07	10	
Melinis minutiflora	Decid. forest	6	1.04	0.77	10	Mosse et al. (1973)
Melinis minutiflora	Brazilian cerrado	3	0.38	0.16	10	
Centrosema pubescens	Brazilian cerrado	2	0.29	0.02	10	
Paspalum notatum	Brazilian cerrado	2	0.30	0.04	10	
Centrosema pubescens[b]	Wheatfield	13	3.88	1.67	4	Crush (1974)
Stylosanthes guyanensis[b]	Wheatfield	13	1.63	0.47	4	
Trifolium repens[b]	Wheatfield	13	2.57	1.56	4	
Lotus pedunculatus[b]	Wheatfield	13	2.01	2.54	4	
Lolium perenne[b]	Wheatfield	13	10.40	10.00	19	
Lolium perenne[a]	Tussock grassland	4	0.11	0.02	17—26	Crush (1973)
Lolium perenne[a]	Tussock grassland	8	0.08	0.10	17—26	
Dactylis glomerata[a]	Tussock grassland	4	0.17	0.02	17—26	
Dactylis glomerata[a]	Tussock grassland	8	0.11	0.12	17—26	
Anthoxanthum odoratum[a]	Tussock grassland	4	0.19	0.02	17—26	
Anthoxanthum odoratum[a]	Tussock grassland	8	0.15	0.41	17—26	
Glycine max	Arable	50	2561	1271	23	Ross (1971) and Ross and Gilliam, (1973)
Glycine max	Arable	162	2406	2282	23	

[a]Shoot dry weights.
[b]Total fresh weights.

mechanisms whereby VA mycorrhizal infection increases P uptake and the source of the extra P entering mycorrhizal plants from soil. These attempts have considered explanations based on changed root physiology, the provision of an increased absorbing surface, and better utilization of insoluble phosphate.

One mechanism is purely physiological. Mycorrhizal root segments of onions grown in sand given ^{32}P-labelled nutrient solution accumulated 25 times more radioactivity in 43 hours than non-mycorrhizal portions of roots on the same onion plants and 500 times more radioactivity than roots of non-mycorrhizal plants (Gray and Gerdemann, 1969). VA infection therefore confers on roots a greater avidity for phosphate. That the accumulation of ^{32}P was directly attributable to the fungus was demonstrated when the fungitoxicant PCNB (pentachloronitrobenzene) was added to the sand 48 hours before the ^{32}P was added. The PCNB drastically reduced the radioactivity in the mycorrhizal but not in the non-mycorrhizal roots. Autoradiography studies (Ali, 1969; Bowen et al., 1975) showed a concentration of ^{32}P inside the fungus within infected roots.

A second way that VA mycorrhizal infection may aid phosphate uptake is by increasing the absorbing surface of the root, the external hyphae being somewhat analogous to root hairs. Baylis (1970, 1972) described a series of plant species where the degree of root hair formation was inversely correlated with an increasing dependence of the plants on mycorrhiza and directly correlated with their ability to absorb P from soils deficient in soluble phosphate. Adding soluble phosphate to such soils overcame the plants' dependence on mycorrhiza. The threshold level of phosphate available for plant growth was thus related to the extent of intimate contact between root and soil.

Considering that more than 95% of the P in unamended soil may be virtually unavailable to plants, it is tempting to suspect that certain microorganisms, including the mycorrhizal fungi, can tap some of this P (see Hayman, 1975a). Certain sparingly soluble inorganic forms of P have in fact been found to be more readily utilized by plants when their roots were mycorrhizal. Murdoch et al. (1967) found growth differences between maize plants with and without mycorrhiza were greater in soil amended with tricalcium phosphate or rock phosphate than in unamended soil. However, when soluble (monocalcium) phosphate was added to the soil the plants grew best of all, irrespective of whether they were mycorrhizal. Daft and Nicolson (1966) found mycorrhizal tomato plants grew better than non-mycorrhizal ones in dune sand supplied with small and intermediate amounts of bonemeal. Hayman and Mosse (1972b) found onion plants with mycorrhiza grew better than those without when given rock phosphate, but with monocalcium or organic phosphates all plants grew well. Apparently the organic phosphates were readily hydrolysed by enzymes from the roots, mycorrhizal or not, and their associated microflora.

The best way to determine whether plants with VA mycorrhiza can tap sources of insoluble soil phosphate that non-mycorrhizal plants cannot is to grow them in soil equilibrated with ^{32}P. Here the readily soluble P (the phosphate in the soil solution and on the exchangeable sites, also called labile phosphate) becomes labelled whereas some of the insoluble P is believed to stay unlabelled and the remainder only weakly labelled. If mycorrhizal plants grown in such soil should acquire a lower proportion of ^{32}P in the total P absorbed (specific activity) compared to non-mycorrhizal plants, this would imply relatively more utilization of the insoluble P by plants with mycorrhiza. Unexpectedly, Hayman and Mosse (1972a) found that mycorrhizal and non-mycorrhizal onion plants took up P with the same specific activity in each of the eight soils that they tested, even in those soils where the mycorrhizal plants had taken up much more total P and were much bigger than the non-mycorrhizal plants. The specific activities of the P varied between soils because the soils ranged widely in their levels of soluble P — the more soluble P, the lower the proportion of ^{32}P in the pool of labile P. Sanders and Tinker (1971) obtained similar results in one of these soils throughout the period of plant growth, even though the mycorrhizal plants again took up more total P. Ross and Gilliam (1973) determined yields of soybeans grown in soil supplied with different forms of phosphate and reached the same conclusion as Hayman and Mosse (1972a) and Sanders and Tinker (1971), namely that the principal form of soil phosphate used by VA mycorrhizal plants is the one most available to plants irrespective of whether they have mycorrhiza. It is deduced from these studies that mycorrhizal roots exploit more of the soluble P than non-mycorrhizal roots because the external hyphae of the endophyte extend beyond the zone of phosphate depletion that develops around roots. This zone arises because the plant absorbs P much more rapidly than it is replenished at the root surface by diffusion due to the poor mobility of phosphate ions in soil. The presence of a phosphate-depletion zone largely over-rides physiological differences between roots with and without mycorrhiza except in soils containing much soluble phosphate where P availability at the root surface keeps pace with its uptake by the root. The improved growth of mycorrhizal plants given sparingly soluble forms of P is probably accounted for by better contact between hyphae and the surfaces of particles of insoluble P than between roots and these particles. This would result in a more efficient absorption of phosphate ions dissociating chemically at these surfaces.

The number of connections between the VA endophyte inside the root and its external mycelium in the soil has been calculated (Bieleski, 1973; Sanders and Tinker, 1973) to be sufficient for the increased flow of phosphate ions into roots that are mycorrhizal to be accounted for by transfer through the hyphae. Translocation of ^{32}P by VA hyphae across at least 15 mm of soil and into an infected root has been demonstrated (Hattingh et al., 1973). This distance is much greater than the phosphate-depletion

zone around roots which is around 1 or 2 mm across.

Further studies now indicate that even though the main benefit of VA mycorrhizal infection to the phosphate nutrition of a plant is to enable it physically to tap more soluble P in soil, there are some soils where a threshold level of P exists below which certain plants, even some with abundant root hairs, can take up no P unless they are mycorrhizal. Mosse et al. (1973) found this to be so with *Paspalum notatum* and *Centrosema pubescens* grown in ^{32}P-labelled Brazilian soils which were extremely deficient in phosphate. Mycorrhizal and non-mycorrhizal plants of *Melinis minutiflora* in contrast, whose roots were very hairy like those of *P. notatum*, took up P with the same specific activity from a similar Brazilian soil. These results suggest that mycorrhizal roots or hyphae may sometimes absorb phosphate present in the soil solution at concentrations inaccessible to uninfected roots. This attribute might improve a mycorrhizal root's ability to compete with bacteria and the hyphae of non-VA fungi for low amounts of soluble soil phosphate.

Apart from increasing phosphate uptake, VA endophytes can also improve the uptake of certain other ions from soil. In zinc-deficient soil in California, for example, peach seedlings were able to take up much more zinc and grow bigger when they had VA mycorrhiza (Gilmore, 1971). VA mycorrhizae also took up sulphur faster than uninfected roots of red clover and maize growing in sand supplied with nutrient solution containing ^{35}S (Gray and Gerdemann, 1973). Reported differences in concentrations of other elements in plants with and without VA infection are often vitiated by the latter having suffered from P deficiency, thereby making their overall nutrition abnormal. Comparisons between plants given either mycorrhiza or phosphate would be more realistic and might reveal differences in soils deficient in certain other trace elements besides zinc. There is no confirmed evidence that VA endophytes can fix atmospheric nitrogen. Resistance to water transport was decreased by VA infection in soybeans, an effect attributed to their nutritional status being improved by the fungus (Safir et al., 1972).

Occasionally the VA endophyte may be slightly detrimental to the host. This appeared so with onions when plant growth was limited by low light and low temperature (Hayman, 1974) or by low temperature alone (Furlan and Fortin, 1973). Also Crush (1973) found that although *Rhizophagus tenuis* enhanced the growth of three grasses in very phosphate-deficient soil, the grasses all grew better without the fungus in slightly more fertile soil (see Table I). Mosse (1973b) found that in some soils given much phosphate onions grew worse with mycorrhiza than without. This was attributed to the build-up of supraoptimal concentrations of phosphate in the plant tissues. In sand and water cultures "Sporokarpienmycorrhiza" slightly decreased growth of maize, although "Vesikelmycorrhiza" significantly increased it (Meloh, 1963).

It is quite likely that VA mycorrhiza affects the hormone balance in the

host root, as occurs with ectomycorrhiza (see Slankis, 1973), but this has so far not been studied. The earlier flowering of tomato, petunia, strawberry and maize (Daft and Okusanya, 1973b) and of cotton (Rich and Bird, 1974) when they are mycorrhizal may be partly a hormone effect. Changes in carbohydrate levels and the presence of fungal carbohydrates such as trehalose and mannitol have not been detected in roots when infected with *Endogone* (Hepper and Mosse, 1973; Hayman, 1974; Bevege et al., 1975). Starch is reported to disappear from infected cells.

Whether most nutrients, particularly phosphate, are transferred from fungus to host by secretion from hyphae and intact arbuscules or by digestion of arbuscules is at present uncertain. Electron micrographs (Scannerini and Bellando, 1968; Kaspari, 1973; Mosse, 1973a and unpublished; Cox and Sanders, 1974) suggest that transfer of material can occur in oil globules (also observed with the light microscope) and exocytotic vesicles from intact arbuscules and that pieces of membrane from the fungus may be incorporated into the host cytoplasm at the granular stage of arbuscule breakdown ("digestion"). The cytoplasm in the arbuscules may retreat behind successively produced septa back into the main hyphae before digestion occurs.

The main effect of the host plant on the fungus is clearly the provision of a home because, according to present knowledge, *Endogone* is an obligate symbiont. Its hyphae are known to grow in soil or on agar only while they are attached to a root or a germinating spore. The hyphae can, however, respond to nutrients in agar and hyphae attached to living roots of plants in monoxenic culture were stimulated by inositol and glycerol (Mosse, 1972c).

Carbon compounds are transferred from host plant to fungal endophyte. Ho and Trappe (1973) grew plants in an atmosphere containing $^{14}CO_2$ and found radioactivity in the fungus, including the spores formed on the external mycelium. The absence of specific fungal sugars and the visually small amount of fungus relative to host tissue suggest there is no carbon sink comparable to the ectomycorrhizal sheath. Nevertheless, ^{14}C compounds from the host can accumulate in the external hyphae of the fungus in proteins, organic acids and cell wall material (Bevege et al., 1975). The carbohydrate metabolism of VA mycorrhiza thus appears to differ fundamentally from that of ectomycorrhiza.

3.7. Interactions with other microorganisms

Interactions between VA fungi and other soil organisms may occur widely. At least one root pathogen is inhibited by VA mycorrhiza. Baltruschat and Schönbeck (1972) observed fewer chlamydospores of *Thielaviopsis basicola* formed on mycorrhizal than on non-mycorrhizal roots of tobacco inoculated with the pathogen. The numbers of spores were inversely correlated with the amounts of VA infection. Mycorrhizal root extracts added

to malt agar cultures of *T. basicola* inhibited chlamydospore production by 80 to 100%. This was largely attributed to the amino acid arginine which accumulated in the endomycorrhizae (Baltruschat et al., 1973). The pathogen decreased the weights of non-mycorrhizal plants by 64% but weights of mycorrhizal plants by only 28%. On the other hand *Phytophthora* root-rot of disease-susceptible but not disease-tolerant soybeans was increased by VA mycorrhiza (Ross, 1972). This may have been because the *Endogone* species in these experiments produced large vesicles in the root cortex which could have caused some splitting of tissues, thereby facilitating entry of the pathogen. Other species of *Endogone* may not have had this effect. VA infection can also increase a plant's susceptibility to virus diseases (Schönbeck and Schinzer, 1972; Daft and Okusanya, 1973a). This is probably an indirect nutritional effect, the better nourished mycorrhizal plants providing more amenable conditions for virus growth and multiplication. Nematodes and *Endogone* can adversely affect each other by competing for the same niche and by mutually suppressing each other's reproduction (Fox and Spasoff, 1972). Increased nematode populations may decrease the population of VA fungi (Schenck and Kinloch, 1974). VA mycorrhizae formed in tobacco roots can increase their resistance to root-knot nematodes (Baltruschat, et al., 1973).

Populations of rhizosphere bacteria beneficial to plants can be positively influenced by VA mycorrhiza. Barea et al. (1975) found that phosphate-solubilizing bacteria inoculated onto seeds or seedlings maintained high populations longer in the rhizospheres of roots that were mycorrhizal than of roots that were not. Free-living nitrogen-fixing bacteria decreased in number more slowly around *Paspalum notatum* roots if they were mycorrhizal (Barea et al., 1973). Finally, improved nodulation of mycorrhizal legume roots, presumably because of their enhanced phosphate nutrition, was demonstrated by Asai (Asai, 1944). This important topic is now attracting special attention. Crush (1974) and Mosse (unpublished) have shown greatly improved nodulation of legumes grown in phosphate-deficient soil when their roots were mycorrhizal, even though the root systems of non-mycorrhizal plants were of similar size. In Brazilian cerrado soils amended with rock phosphate, nodulation and nitrogen fixation in *Stylosanthes*, *Centrosema* and *Trifolium* only occurred to any extent in the plants that were mycorrhizal. Rock phosphate alone stimulated plant growth less than mycorrhiza alone and the two treatments together acted synergistically, resulting in a 7 to 22 fold increase in dry weight (Mosse et al., 1976). If results such as these obtained with legumes in pot experiments could be emulated under field conditions, they would have a large economic impact on tropical agriculture.

3.8. Practical considerations and conclusions

Most of the growth experiments with VA mycorrhiza have been done with single isolates of *Endogone*. However, it is now evident, largely due to the work of Dr. Barbara Mosse at Rothamsted, that the various species of *Endogone* differ in the extent to which they stimulate plant growth. This specificity is related more to soil type than to the species of host plant, the most effective *Endogone* species in one soil, for example, being surpassed by four others on the same host in another soil (Mosse, 1972a, b, 1973a).

Pot experiments with unsterilized soils (Mosse et al., 1969; Mosse and Hayman, 1971) showed that the indigenous VA fungi, although capable of heavily infecting plant roots, sometimes did not stimulate plant growth whereas an introduced species did. The existence of such differences and the successful introduction of a selected *Endogone* species into an unsterile soil are of obvious practical significance. In soils where the indigenous VA population is small or ineffective, mycorrhizal inoculum could be introduced at sowing or by pre-inoculating plants that are normally transplanted as seedlings or cuttings. The means of producing suitable inoculum in large quantities for this purpose, as is possible with *Rhizobium*, needs to be investigated further.

Few field experiments have been done with VA mycorrhiza. Khan (1972) obtained growth increases with maize inoculated with *Endogone* in the field. The introduction of *Endogone* into small field plots (1.5 m^2 bins) of soybean (Ross and Harper, 1970) and into a citrus nursery (Kleinschmidt and Gerdemann, 1972) overcame the deleterious effect of soil fumigation on plant growth in the absence of large applications of phosphate fertilizer. Inoculation of soybean seedlings with *Endogone* before transplanting to fumigated field plots increased seed yield of a nodulating but not of a non-nodulating isoline (Schenck and Hinson, 1973).

Various practical considerations of VA mycorrhiza are outlined by Gerdemann (1975). The possible depletion of the soluble soil phosphate by *Endogone* must be taken into account under agricultural conditions because the P is not recycled as in natural ecosystems. Therefore experiments with mycorrhiza combined with cheaper forms of phosphate fertilizer such as rock phosphate (cf. Jackson et al., 1972) or low levels of superphosphate fertilizer, or in soils containing much residual fertilizer phosphate, may be more realistic than tests in unamended soil.

From both the practical and academic points of view, the greatest challenge in VA mycorrhizal studies is to grow the endophyte in pure culture. Once this is achieved, large-scale inoculations will become much more feasible for the practical man and fundamental studies of host—endophyte interactions will appear more enticing to the purist.

4. ORCHIDACEOUS MYCORRHIZA

4.1 Occurrence

Endomycorrhiza in the Orchidaceae is a distinct type of mycorrhiza restricted to this one plant family. Its unique properties distinguish it from all other mycorrhizae except perhaps the mycorrhizal infections in the Gentianaceae and in the bryophyte *Aneura* (see Harley, 1969). Despite its taxonomic limits orchidaceous mycorrhiza has attracted much attention, especially from physiologists. Orchids are of particular relevance to studies of mycorrhizal relationships because they are all saprophytic during at least part of their life and at that time, they are obligately mycorrhizal under natural conditions. Although the orchids are only a minor component of temperate floras, both in size and number, they abound in the tropics where some of the saprophytic species can cover a whole tree. Their economic value is mainly ensured by the constant appeal of Vanilla essence to the palate and of their floral beauty to romance.

4.2. The fungal endophytes

The fungi that form endomycorrhizae with orchids are particularly intriguing because two of the major ones, *Armillaria mellea* and *Rhizoctonia solani*, are species well known to include a number of virulent strains pathogenic on many higher plants. Unlike other mycorrhizal fungi, most fungal endophytes of the Orchidaceae can be readily isolated and maintained in pure culture. They grow more rapidly than other mycorrhizal fungi and are good saprophytic competitors. They are usually basidiomycetes with clamp-connections in their hyphae, or species of *Rhizoctonia*, several of which have been induced to form their perfect basidial stages in culture. Burgeff (1936) isolated mainly clamp-forming basidiomycetes from colourless saprophytic orchids and species of *Rhizoctonia* from green orchids. Studies describing the isolation and identification of the fungal endophytes are comprehensively reviewed by Harley (1969). The perfect stages of many of the *Rhizoctonia* symbionts were identified by Warcup and Talbot (1967) as species of *Ceratobasidium*, *Sebacium*, *Thanatephorus* and *Tulasnella*.

As is to be expected with unspecialized parasites, strains of *Rhizoctonia solani* and other species isolated from particular orchids or even from non-orchid hosts are not generally restricted to the one species of host plant. For example Hadley (1970) tested 32 isolates of *Rhizoctonia* obtained from orchids, non-orchid hosts and soils from different parts of the world and found no evidence of any species-to-species limitation between orchid and fungus. Some orchids, especially *Dactylorhiza purpurella*, formed endomycorrhiza with many or most fungal isolates tested, whereas others such as *Spathoglottis plicata* formed mycorrhiza with only a few. The fungi

themselves vary in their symbiotic range. *Tulasnella calospora* is possibly a universal orchid symbiont whereas others, including *Thanatephorus cucumeris*, are confined to a few orchid species. Warcup (1973), however, found some specificity in the symbiotic germination of certain Australian orchids on agar containing powdered cellulose as the carbon source. For example *Pterostylis* spp. were stimulated to germinate by *Ceratobasidium cornigerum* only, and *Diuris* spp. by *Tulasnella calospora* only, while *Thelymitra* spp. were generally stimulated by several *Tulasnella* spp. but not by *C. cornigerum*. The capacity of *T. calospora* to stimulate germination varied significantly.

Downie (1957) obtained isolates of *R. solani* parasitizing cauliflower and tomato which were symbiotic with *Orchis purpurella*. Harvais and Hadley (1967a) isolated four strains of *R. solani* pathogenic to crop plants, of which those from tomato and rice stimulated growth of *Orchis purpurella* protocorms, the one from wheat formed an ineffective infection in the orchid, and the one from potato was parasitic on the orchid. The hyphae of *Ceratobasidium cornigerum*, formerly *Mycelium radicis goodyerae repentis*, are widely distributed beyond woodlands where the orchid *Goodyera repens* grows (Downie, 1943).

4.3. The infection

In natural conditions orchid embryos normally become infected in the early protocorm stage. Usually the central region of the embryo becomes fully colonized by the fungal endophyte, then differentiation of epidermal hairs and an apical meristem lead to the formation of a protocorm. As a vascular cylinder is formed the fungus becomes restricted to the cortex. Hyphae connect the cortical infection with the mycelium in the external substrate. Characteristic hyphal coils, also called pelotons, are formed in many cells and several of these become digested, especially in the central region of the embryo, leaving granular masses of intracellular fungal material. As young roots are formed on the protocorm they become infected from fungi in the surrounding soil, not from the fungus in the protocorm. For more information on the establishment and appearance of mycorrhizal infection in orchid embryos and seedlings the detailed accounts of Bernard (1909), Burgeff (1936) and Harley (1969) should be consulted.

Certain climbing orchids have long roots which are almost uninfected and short roots which are usually heavily infected but short-lived. Some roots have zones where the fungus remains healthy and other zones where it is digested. Orchid roots usually have a dense internal infection but compared to other mycorrhizae they generally have fewer and simpler connections with the external mycelium in the soil. New roots formed on the adult plants in the growing season become infected from the soil and individual cells may show repeated invasion by and digestion of the fungus throughout the season.

4.4. Host—endophyte interactions and physiology

In some orchid seedlings the fungus becomes parasitic and kills the plant; in others digestion of fungal hyphae seems to help keep the fungus at bay and provide nutrient materials for the plant; in yet others the fungus may be overdigested and die out (Bernard, 1909; Williams and Hadley, 1970). Even in mature orchid plants the balance between parasitism and symbiosis can be tenuous. For example Alconero (1969) obtained mycorrhizal and pathogenic infections of *Rhizoctonia solani* in Vanilla orchid roots, the two types of infection often appearing near each other. The factors leading to the establishment of one or other type of infection were not resolved, although age of plant tissues and nutrition of the fungal inoculant were implicated. Moreover, infection of the Vanilla orchid roots with *R. solani* sometimes predisposed them to infection by *Fusarium oxysporum* f. sp. *vanillae* (Alconero and Santiago, 1969).

The fungal endophyte in some orchids may also infect adjacent trees and shrubs so that the orchid obtains much of its nourishment from the woody plant by means of the fungus they share. Such epiparasitism is reminiscent of the ericalean mycorrhiza of *Monotropa* (see Section 2.4). It has been shown to occur in epiphytic and saprophytic orchids. In fact many of the orchids classed as saprophytes may turn out to obtain their nutrients epiparasitically from green plants rather than saprophytically from dead organic matter (Harley, 1969). The saprophytic orchid *Gastrodia minor* has been shown to be epiparasitic on *Leptospermum scoparium* in New Zealand (Campbell, 1963). The fungus which penetrates the cells of *G. minor* non-pathogenically and undergoes partial digestion in them also infects adjacent roots of *L. scoparium*, causing cortical damage.

The Orchidaceae form a series of increasing saprophytism, more striking than in the Ericales, and this is correlated with an increasing intensity and complexity of endomycorrhizal development. Infection by and digestion of the endophyte is particularly common in the saprophytic orchids, whereas green orchids may be almost uninfected in the adult stage.

Synthesis of DNA can be induced in the cortical cells of orchid roots that are mycorrhizal. Williamson (1970) found nuclei with two to four times the normal DNA content in infected and adjacent healthy cells.

Orchid seeds are minute, containing limited food reserves and embryos that are little differentiated. They are therefore dependent for their early growth on external supplies of organic carbon compounds, until such time as photosynthesis begins. Although some orchids can be raised without mycorrhiza in pure culture, given the right nutrient conditions including sugars and vitamins (see Harvais and Hadley, 1967b; Harley, 1969), they obtain their initial carbon supplies in nature from their fungal endophyte. Their dependence on the fungus varies according to the extent to which their carbon nutrition is saprophytic or perhaps epiparasitic, but even

photosynthetic orchids which are self-sufficient for carbon when mature must rely on mycorrhizal help during their early growth. Penetration of the embryo by the fungal endophyte can in some instances greatly stimulate growth, as in the orchid *Phalaenopsis amabilis* which grew much more rapidly after infection than before (Bernard, 1909).

The carbon nutrition of orchidaceous mycorrhiza has been much studied. The fungal endophytes can use complex carbohydrates much more readily than many other fungi, including the ectomycorrhizal basidiomycete fungi. This may partly explain the typical habitats of orchids being rich in decaying organic matter. However they can also readily use simple sugars such as glucose and sucrose and grow rapidly on agar containing these substances. Smith (1966) demonstrated the ability of *R. solani* from terrestrial European orchids to use cellulose, and *Armillaria mellea* can utilize both cellulose and lignin. In aseptic cultures of orchid and fungal symbiont the source of carbon can affect the balance between symbiosis and pathogenesis. In such cultures Hadley (1969) found that 1% cellulose in the medium enhanced the development of the protocorm and led to a more controlled growth of the endophyte and less chance of parasitism and death of the orchid, compared to glucose as a carbon source which caused the fungus to become too vigorous and swamp the orchid. The ability of the fungal endophyte to break down complex carbon compounds such as cellulose seems to be its main benefit to the host plant. The role of the fungal endophytes in the stimulation of orchid growth and in the utilization of complex carbohydrates is thoroughly discussed by Harley (1969) and will not be described further here.

The orchid endophytes can readily use organic nitrogen compounds in addition to inorganic nitrogen. The possible role of these fungi in aiding phosphate uptake by mature plants growing in P-deficient soil awaits investigation.

Sugars may enter the root as products of fungal hydrolysis of complex carbohydrates in the external medium or more probably by translocation in the fungal hyphae and subsequent release into the orchid tissues. Burgeff (1936) estimated about 32,000 hyphal connections between adult *Platanthera* plants and soil. These had a diameter of 4 μm and were judged sufficient for conduction of food materials. Translocation of nutrients through the hyphae is well documented. Smith (1966, 1967), using the split plate with diffusion barrier method, showed that *Rhizoctonia repens* could translocate ^{32}P in KH_2PO_4 and ^{14}C in glucose from the external medium into the tissues of seedlings of *Orchis purpurella*. Infected tissues of the orchid contained both host sugars (glucose, fructose and sucrose) and fungal carbohydrates (glucose, trehalose and mannitol). The host could convert fungal trehalose to sucrose. Nutrient materials are probably exchanged between fungus and plant through intact membranes as well as during digestion. The latter is also considered to be a defence mechanism of the host to prevent excessive invasion by the fungus.

Hijner and Arditti (1973) suggest that exchange of vitamins between orchids and endophytes is important in their symbiotic relationship and in their co-evolution. They isolated a *Rhizoctonia* sp. from the orchid *Cymbidium* that produced the pyrimidine moiety of thiamine which may enhance the growth of certain orchid seedlings. Conversely *p*-aminobenzoic acid produced by orchid seeds could satisfy the vitamin requirements of the fungus.

The provision by the host plant of an ecological niche for the fungus is less important in orchidaceous than in other mycorrhizae because the orchid endophytes are also strong saprophytes and virulent pathogens on other plants. One of the most obvious actions of the host plant on the fungus is its digestion of the fungal hyphae. This helps limit the spread of the fungus and keeps its latent pathogenic abilities in check. Another strongly inhibitory effect of the host plant on its endophyte is through the production of an antifungal compound termed orchinol. This is a phenolic substance described by Gäumann and Kern (1959). Orchid tubers, which are resistant to infection, produce much larger quantities of orchinol than orchid roots, which are not. The substance is considered to be somewhat analogous to phytoalexins in other plants which can be produced in response to contact with or invasion by some fungi. Certain fungi not endomycorrhizal with orchids, and even bacteria, could induce the formation of orchinol in orchids. The substance was inhibitory to some soil fungi but not to others. The amounts of orchinol produced can be quite large and studies on the mechanisms leading to its synthesis would be relevant to studies on phytoalexins and phenolic compounds in general in relation to biological control of plant pathogens.

4.5. Conclusions

Orchidaceous mycorrhizae clearly differ considerably from other mycorrhizae, especially in their nutrition. The links between them and other endomycorrhizae might be strengthened by further studies of the family Burmanniaceae. That family, which together with the Orchidaceae constitutes the order Microspermae, includes saprophytic plants with both septate and aseptate fungal endophytes (Van der Pijl, 1934). The orchidaceous mycorrhizae provide a good system for investigations on the transfer of organic compounds between organisms and have received much attention in this respect, particularly at the seedling stage, which has led to a better understanding of symbiosis. Another efficacious line of study would be the mineral, especially phosphate, nutrition of naturally occurring green orchids, in view of the marked emphasis on this in other types of mycorrhiza.

5. THE SIGNIFICANCE OF ENDOMYCORRHIZA

It is only recently that the significance of endomycorrhiza has really begun to be appreciated; microbiology and plant physiology textbooks

of no great vintage have often barely recognised it. The unreality of ignoring root endophytes when considering plant growth in soil is now evident from the effects of endomycorrhizae on nutrient uptake and from their ubiquity such that plants in many situations may not strictly speaking have roots but mycorrhizae (see Wilhelm, 1966).

The term "endomycorrhiza" is somewhat misleading because it implies a single category of fungus–root associations. It really refers to a broad spectrum of symbiotic fungus–root associations where the fungi are unrelated taxonomically, the anatomy of the infected roots varies widely, and the physiological interactions between root and endophyte can differ markedly. Although there are obvious similarities between the groups of endomycorrhiza, it is incorrect to assume that what is true for ericalean mycorrhizae may also be true for vesicular–arbuscular or orchidaceous mycorrhizae and vice versa.

Fungi that infect plant roots form associations of variable duration and different degrees of impairment to the plant. Where such infections are most permanent and most benign there is a state of balance. Such a balanced relationship between two organisms is believed to represent a peak of naturally evolved coexistence. Unbalanced relationships, where the host plant is damaged by the fungal parasite, are considered more primitive. The balanced stability of the endomycorrhizal system is apparent in that it is not greatly upset under unnatural conditions such as in monocultures of single genetic varieties of plants in agriculture. This contrasts with pathogenic fungi which usually do not cause much disease when they are evolved as an integral part of a natural ecosystem but can rapidly proliferate and cause epidemics in agricultural crops. That the mycorrhizal balance represents a state of dynamic equilibrium and can be upset if one or other partner is too demanding, however, is evident in the orchidaceous mycorrhizae. Here the balance is the least stable of the endomycorrhizal associations and there is often a mutual struggle where the fungus may kill the orchid seedling or may itself be discarded by the plant. A recent detailed account of dual organisms and the concept of biotrophy ranging from parasitism to (mutualistic) symbiosis is that of Lewis (1973).

Infection of plant tissues without visible destruction is not unique to mycorrhizal fungi. The symptomless infection in *Lolium* plants is well known. Wheat roots can be harmlessly colonized by the avirulent parasite referred to as *Phialophora radicicola* (Scott, 1970). The balansioid fungi can infect their gramineaceous host plants systemically but usually only visibly damage the reproductive parts (see Diehl, 1950); the loose smuts behave in a similar manner. An infection that does not cause necrosis but merely prevents the setting of seed is not necessarily disadvantageous to some grasses which have an efficient means of vegetative reproduction.

With endomycorrhizae there is now much experimental evidence that not only are the host plants not disadvantaged by the fungal infection,

but also that in certain situations the infection confers a selective advantage. Thus it is normally a beneficial, symbiotic fungus—root association and evidence of pathogenic effects is rare. Occasionally the host plant may be adversely affected by the endophyte as when light and temperature conditions are very unfavourable for plant growth (see Hayman, 1974) or when the soil is extra rich in nutrients for a particular plant (see Bannister and Norton, 1974; Crush, 1973; Mosse, 1973b). Otherwise the general lack of any harmful effect of VA mycorrhizae, even in soils containing adequate soluble phosphate for the host plant, suggests a negligible carbohydrate drain on the host by the fungus or a compensating mechanism that favours the host in other ways besides stimulating nutrient uptake. The production of growth factors by the fungus, as in ectomycorrhizae, is one obvious possible mechanism and should be investigated.

Carbon relationships between roots and their endomycorrhizal endophytes have received much attention with orchids where the system is readily grown under aseptic conditions and where the nutrition of the fungus can be evaluated separately. Their ability to convert complex carbohydrates such as cellulose to simple sugars such as glucose distinguishes them from ecto- and other endomycorrhizae. Their production of the fungal carbohydrates trehalose and mannitol is characteristic of mycorrhizae involving basidiomycete or ascomycete fungi, i.e. the ecto-, ericalean and orchidaceous mycorrhizae, but not of mycorrhizae involving "phycomycetes", i.e. the V A mycorrhizae. There is some evidence that the latter may be able to obtain certain carbon compounds externally to supplement those available inside the root. This evidence includes the demonstration that growth of the external mycelium is increased by inositol in the medium of two-membered cultures, the observations of VA fungal hyphae growing into particles of organic matter in soil, and the presence of similar phycomycetous endophytes in saprophytic members of the Burmanniaceae and saprophytic pteridophyte prothalli where carbon must enter the dual organism from the substrate in the absence of photosynthesis.

Most work on host—endophyte interactions in VA mycorrhizae has been concerned with the function of the intact system in soil. This is probably because the physiology of the fungal endophyte cannot be readily examined either as a pure culture or even as a detachable mass of mycelium such as the ectomycorrhizal sheath, and because of the dramatic effect of the infection on phosphate uptake in P-deficient soils. The ability to take up extra phosphate from nutrient-poor soils is characteristic of VA, ericalean and ectomycorrhizae. It may be a general feature of all mycorrhizae because orchid mycorrhizae, although not yet examined in soil, have been shown to translocate ^{32}P through the external hyphae into the root in vitro.

There is no confirmed evidence that any of the endomycorrhizae fix nitrogen. However, VA mycorrhizae may stimulate nitrogen-fixing bacteria in their rhizospheres and they enhance nodulation and nitrogen fixation

by *Rhizobium* in legume roots. Mycorrhizal infection in orchids and ericaceous plants may enable them to utilize organic nitrogen in soil. The uptake of certain trace elements is influenced by VA mycorrhizae and soils deficient or toxic in specific elements should be examined in this respect.

Much of the increased uptake of certain ions from soil by roots that are endomycorrhizal is accounted for by the external mycorrhizal hyphae enabling the root to explore more soil. The three types of endomycorrhiza all form a mycelial network in the soil around plant roots and all have been shown to translocate nutrients into the roots. These features give the group a certain unity. Another characteristic the endomycorrhizae have in common is that the fungus is restricted to the root cortex and does not penetrate the endodermis or stele. Thus all endomycorrhizal roots have a cortical infection directly linked to a network of hyphae in the soil. The three types of endomycorrhizae are also characterized by an extensive intracellular as well as intercellular development inside the root. Most endomycorrhizal infection occurs typically in the short-lived, unsuberized fine roots, e.g. the lateral roots of VA mycorrhizae, the short roots of climbing orchids, and the delicate hair roots of the ericoid mycorrhizae. It is absent from chlorophyll-containing tissues and from storage tubers, e.g. when these are modified shoots as in potatoes or underground stems as with orchid rhizomes.

One of the most obvious benefits to the fungus in the endomycorrhizal association is that it is provided with a unique ecological niche where it is well and continuously nourished and where the internal phase does not encounter competition and antagonism from other soil fungi and bacteria. The avid competition between microorganisms for substrate is perhaps the major factor limiting their activities and in soil the majority at any one time are starved and intimidated into dormancy by others feeding on the same food source and in some instances also producing antibiotic substances. Thus nutrient availability enables endomycorrhizal fungi to achieve a larger and more functional biomass in more intimate contact with the root and thus increases their chances of exerting a greater effect on plants than other microbial species restricted to the rhizosphere or beyond.

The fungal endophyte cannot, however, expect a free ride in the root and often has to contend with being digested. Digestion of fungal structures is a feature common to the three types of endomycorrhiza but not to ectomycorrhiza. It occurs continuously in endomycorrhizae, usually at a fairly constant rate that does not upset the balance, but it can be especially aggressive in orchids such that the plant is sometimes considered to be parasitic on the fungus. There are different opinions on the function of digestion, mainly concerning the degree to which it is either a defence mechanism of the host or a nutritive mechanism for transfer of materials. Digestion cannot be an indispensable means of transfer of substances from fungus to host because transfer occurs perfectly well without it in ectomycorrhizae and in certain pathogenic fungal infections. Furthermore, only

materials in the pelotons or arbuscules are likely to be released during digestion and only during the limited period the process is occurring, whereas secretion from actively growing hyphae would provide a continuous supply of materials. However, the production of pelotons and arbuscules greatly increases the area of contact between fungus and host cell and hence provides more opportunity for nutrient transfer by secretion before the onset of digestion. In short there must be movement of materials from intact hyphae, including hyphal coils and arbuscules, as well as during digestion, but the relative importance of each remains to be elucidated.

The microbial population around endomycorrhizae in soil is likely to differ from that in the rhizosphere around an uninfected root because the fungal endophytes affect the physiology of the root and consequently probably affect root exudation and the organisms these exudates stimulate. Indeed endomycorrhizal roots can prolong the existence of bacteria introduced around them, including those which dissolve insoluble phosphates, fix nitrogen or perhaps produce growth substances. This may affect plant growth beyond the mycorrhizal effect per se. Interactions between the sterile mycelia on root surfaces and the external endomycorrhizal hyphae may also be important. Interactions between endomycorrhizal and plant pathogenic fungi in the rhizosphere have important implications in biological control (see Wilhelm, 1973). This may occur by competition between symbionts and pathogens for similar ecological niches and by effects on root physiology. The latter is most obvious in orchids which produce orchinol in their roots. In root disease studies the whole syndrome of microorganisms associated with roots should be recognised, including pathogens, symbionts, rhizoplane and rhizosphere fungi and bacteria, and nematodes.

Lack of specificity in host range between an endomycorrhizal endophyte and its host plant is a characteristic of ericalean, VA and to a large extent orchidaceous mycorrhizae. Isolates of most endomycorrhizal fungi have readily been inoculated onto several host species. Such inoculations are of practical significance in unsterile soil because even though endomycorrhiza is usually present in plants growing in most soils, the native infection is not necessarily the most effective one. This has been clearly demonstrated in growth experiments with VA mycorrhizae. The introduction of non-indigenous mycorrhizal species into a habitat can be successful if the introduced species has a good competitive base as when it is inside a plant root. Thus it may be possible to manipulate endomycorrhizal populations qualitatively in addition to the quantitative changes brought about by environmental factors.

Ecologists are now paying more attention than previously to the below-ground components of an ecosystem. In this regard the role of endomycorrhizae in nutrient cycling in natural ecosystems should prove to be a very significant one. Most uncultivated soils are deficient in plant-available phosphate and many plant species have been shown to grow poorly in such

soils when the indigenous mycorrhizal fungi have been eliminated. This is because of the inability of many uninfected plants to take up adequate P for growth. Furthermore there is strong competition for the available phosphate by all the roots and the various microorganisms in the soil. The external endomycorrhizal hyphae may compete for this phosphate more effectively than the roots. They are better able to explore more soil and increase the absorbing surface of the root, and may also take up phosphate at lower concentrations than roots themselves can. Endomycorrhizae may be particularly important in the establishment of seedlings in nature. This is very evident with minute orchid seeds containing immature embryos unready to photosynthesize and applies also to the small seeds of other plants which contain mature embryos but low food reserves. Early infection of the latter by VA fungi could promote early uptake of soil nutrients such as phosphate and so prevent phosphate-deficiency from checking, perhaps irreversibly, the growth of the young seedling.

Plant colonization of industrial wastes such as coal tips to convert them to some aesthetic and recreational value may be another area where endomycorrhizae can play a significant role. These sites are deficient in nutrients and pioneer plants there might appreciate symbiotic aid both from nitrogen-fixing microorganisms and organisms able to improve nutrient uptake from an impoverished medium. The work of Daft et al. (1975) has illustrated some benefits from arbuscule-forming endophytes in such habitats.

The economic significance of endomycorrhizae in crop plants is receiving belated recognition. The ability of root endophytes to improve plant growth in many soils has much practical potential, whether this growth stimulation is of the order of 10% or several 100%. Apart from known horticultural benefits of endomycorrhiza in orchids and perhaps in ornamental Ericales, consideration of the impact of VA mycorrhiza in agriculture is now dominating assessments of the practical use to man of endomycorrhiza. Its presence in most crop plants and its role in plant nutrition, especially in P-deficient, P-fixing and fumigated soils, and with plants that are poor phosphate feeders, are now well established and point to its potential where large-scale applications of increasingly costly superphosphate fertilizer may be unfeasible. The possible use of efficient VA mycorrhizal species in conjunction with smaller quantities of superphosphate or alternatives such as rock phosphate will be the subject of much research during the coming decade.

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