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# Mycorrhiza and plant growth

## 1. INTRODUCTION

Mycorrhizas are mutualistic associations between soil fungi and plant roots. The fungi inhabit living roots, causing very little tissue damage, and are nutritionally biotrophic (LEWIS 1973). Fungal spread within the root system is limited, and usually only the fine absorbing rootlets become mycorrhizal. In all but one group the fungus penetrates into the cells, but the intracellular infection is usually short lived and the host cell survives after collapse of the invading fungus.

Mycorrhizal infections are not separate phenomena clearly demarcated from all other fungal infections of living plants. Under particular conditions their mutualism may not find expression and the more usual growth depressant effect of fungal infection may become operative. There are some interesting analogies (LEWIS 1974) in reaction at the cellular level to infection by mycorrhizal and by more pathogenic fungi. For instance, respiration and the volume of the host cytoplasm increase in infected cells, starch reserves are mobilized, and there is an inflow of carbohydrate to the infection sites. MEYER (1968) stresses the underlying parasitism in his definition of mycorrhizas as'a living together of partners that attack each other but, having attained an equilibrium of struggle, can coexist for more or less prolonged periods. One prerequisite of this partnership is that either partner can intervene in the metabolism of the other without disturbing it too greatly'. Nevertheless, mycorrhizas are mutualistic associations and it has now been demonstrated beyond doubt that they can be beneficial for plant growth.

Since FRANK (1885) first described the specialized modified root structures of the *Cupulifereae* and named them 'mycorrhiza', the term has been greatly extended and now covers an enormous range of root-fungus associations in which the root structure undergoes little change and there is no anatomical evidence of tissue damage or obvious pathogenic effect on plant growth. HARLEY's (1969) detailed account of the biology of mycorrhiza leaves the reader bewildered by the diversity of structures, fungal species, plant families and interactions that occur within mycorrhizal systems. HARLEY warns against the assumption that all these associations necessarily have similar effects on plant growth. Many workers in this field now feel that the general term mycorrhiza is of little

value and that a subdivision into clearly definable types has become essential. The division proposed by LEWIS (1973) into ecto- or sheathing mycorrhiza, vesicular-arbuscular (VA) mycorrhiza, and ericaceous and orchidaceous mycorrhiza will be followed here. Thanks to improved techniques for producing VA and ericaceous mycorrhiza experimentally, enough information has been accumulated during the last decade to permit a tentative outline of mechanisms by which the different types of mycorrhiza affect plant growth (Table 1).

TABLE 1. *Effects of different types of mycorrhiza on the host*

| Mycorrhizal type | Effect on plant growth | Chief nutrients supplied |
|---|---|---|
| V.A. | Improved nutrient uptake | P, Zn, Sr, S, K |
| Sheathing | Improved nutrient uptake* | P, K |
| Ericaceous | Improved nutrient uptake | Organic N, P |
| Orchidaceous | Improved seed germination and flower induction in some saprophytic plants | sucrose, carbohydrate |

* and hormonal effects on root morphology

In view of the diversity of mycorrhizal systems and the very different types of fungi involved (*Endogonaceae* (Phycomycetes) in Va mycorrhiza, Agaricales, Gasteromycetes (Basidiomycetes) and some Ascomycetes in sheathing mycorrhiza, *Pezizalae* (Discomycetes) in ericaceous, and *Rhizoctonia* spp. (Basidiomycetes and imperfect fungi) in orchid mycorrhiza), the functional similarities between the ecologically important groups viz. VA, sheathing and ericaceous mycorrhizas are perhaps surprising. Further study may reveal greater divergence. At the moment, however, the orchidaceous mycorrhizas stand out as being markedly different not only in their function - aiding plant growth during a temporary or permanent saprophytic stage - but also in the organs infected (protocorms, rhizomes, aerial roots and only sometimes terrestrial roots) and in the fungi concerned. Unlike the other mycorrhizal fungi the orchid fungi are cellulose and lignin decomposers. They can be virulent pathogens (*Armilliaria mellea* and some *Rhizoctonia* spp.) for non-orchidaceous hosts and on nutrionally rich media can even kill their own symbiotic partners (BERNARD 1909; WARCUP 1975). In contrast the endophytes of VA mycorrhiza are obligate symbionts with low pathogenic potential, and there is little evidence that the fungi of sheathing or ericaceous mycorrhizas ever have the pathogenic potential of the orchid endophytes.

In all mycorrhizal systems nutrients are transferred from the external medium, which in nature is the soil, to a higher plant by means of a continuous hyphal network based partly in the soil and partly in the root or closely adpressed to its surface. Fig. 1 shows some of the environmental factors that may influence the system. Unlike the other important symbiotic system of the leguminous nodules, which operates by fixing nitrogen from the air, mycorrhizal systems do not add to the total store of nutrients in the soil, though they may increase their availability.

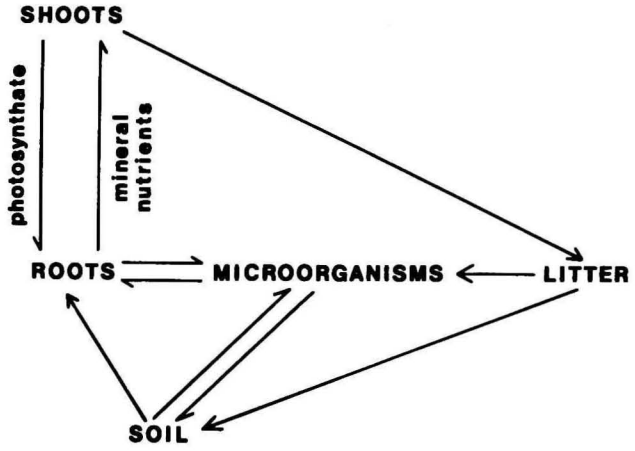



FIG. 1. *Some pathways of nutrient transfer affecting mycorrhizal systems*

Two questions in particular interest ecologists:
1) how widespread are mycorrhizas in natural ecosystems, and 2) how important are they in nutrient uptake and cycling ? In the following an attempt is made to provide some answer or at least to show why a definitive answer to these questions is so difficult.

## 2. THE OCCURRENCE OF MYCORRHIZA

### 2.1. THE HOSTS

It has long been known that in most undisturbed ecosystems roots are normally mycorrhizal (FRANK 1885; SCHLICHT 1889; JANSE 1897; STAHL 1900). Va mycorrhizas have the widest host range and are by far the commonest type. They occur in liverworts, Pteridophytes, some Gymnosperms, and most Angiosperms, but appear

to be absent in the mosses. GERDEMANN (1968) lists fourteen families that are never or rarely mycorrhizal, including *Cruciferae, Chenopodiaceae, Cyperaceae, Juncaceae* and *Caryophyllaceae*. It is widely believed that most trees have sheathing mycorrhizas but this is erroneous. *Pinaceae* and *Fagaceae* are exclusively ectomycorrhizal but many other temperate trees, most *Rosaceae*, sixty-three out of sixty-six tropical tree species in Nigeria (REDHEAD 1968) and many trees in the Amazon rain forest (T. St. JOHN personal communication) regularly have VA mycorrhizas. So do the important tropical tree crops, cocoa, coffee, tea, rubber, and citrus. A few plants, for example juniper, apple, and hazel, can have both VA and sheathing mycoorhizas, but one of these is usually the normal while the other may be site-determined. Sometimes the type of mycorrhiza may change as the host plant matures. For instance poplars, in which DANGEARD (1900) first saw the fungi he described as "vesicular-arbuscular", often have sheathing mycorrhizas when mature (FONTANA 1961). READ *et al.* (1977) recently reported that *Helianthemum chamaecistus* growing in a grassland sward was at first heavily infected with VA mycorrhizal fungi and later formed sheathing mycorrhiza with *Cenococcum* sp.

The most important plants with ericoid mycorrhizas belong to the genera *Erica, Vaccinium, Rhododendron* and *Calluna* (Read & Stribley 1975).

## 2.2. THE FUNGI

VA endophytes are so widely distributed that virtually no soils are reliably free from infection. However, levels of infectivity differ (MOSSE 1977a) and it is now clear that VA endophytes comprise a range of different fungi, so far uncultured. They are distinguished by their characteristic resting spores, often more than 100 µm in diameter, but non-sporing endophytes also exist and are common in forests. Spore numbers are not a reliable measure of root infection in natural situations (HAYMAN 1975, 1978) but often are in experimental systems. Although many of the known endophytes have a world wide distribution, their occurrence within small areas can be localized and is often inexplicable in terms of vegetation or soil differences. Soil pH can be unsuitable for particular species (MOSSE 1972) and species also differ in optimum temperature range (FURLAN & FORTIN 1973). Unlike some other mycorrhizal fungi VA endophytes have very little host specificity and can infect any potential host plant. Low spore mobility may account for the sporadic occurrence of different endophyte species, but this is difficult to reconcile with their world wide distribution. It is hard to believe that this could be man-made in view of the extreme age of VA infections which date back to Devonean fossil plants (BUTLER 1939).

Spores of the agarics, common fungal associates of many sheathing mycorrhizas, are small and wind dispersed. They are often absent from prairie and steppe soils. According to many, more or less well authenticated reports (summarized by REDHEAD 1974), forest soil or pure inocula must be added to

obtain satisfactory growth of introduced trees, particularly *Pinus* spp. (BRISCOE 1959; HACSKAYLO & VOZZO 1967). BOWEN (1963) found that *Pinus radiata* could form mycorrhizas in soils on which eucalypts had grown but such mycorrhizas were less efficient than those formed in soils on which pines had previously grown. Some ectomycorrhizal hosts are relatively restricted in their fungal associates, but others form associations with a wide range of fungi. ZAK (1973) reported over a hundred different mycorrhizal associations of one *Pseudotsuga menziesii* tree. SHEMAKHANOVA (1967) concluded from a survey of Russian work that one- and two-year-old oak seedlings became mycorrhizal, not only in soils long denuded of forests, but also in soils far removed from them.

## 2.3. THE ASSOCIATION

Early investigators strongly believed that mycorrhizal development was linked to the humus content of the soil. More systematic surveys such as those of LIHNELL (1939), STRZEMSKA (1955), REDHEAD (1974), READ *et al.* (1976) have not shown any correlation between levels of Va infection and soil conditions such as pH, humus content or soil type. Mycorrhizal roots are usually most abundant in the top 15-20 cm of the soil (MEYER 1973; READHEAD 1968; SPARLING & TINKER 1975) but this may simply reflect greater root density in the relatively nutrient rich surface layer. Records of percentage infection alone can be misleading and root density, itself related to nutrient levels, must also be taken into account. MEYER (1973) reported that a beech seedling with a split root system formed 500 root tips/100 ml soil in a mull soil and 45,000 in a mor soil. Eighty eight percent of the roots in the mull soil were mycorrhizal and only 51 per cent of those in the mor; the total number of mycorrhizal roots was obviously far greater in the mor soil. Plant species also differ in rooting habit. In a mixed forest stand containing three times as many pines as spruces, more spruce mycorrhiza occurred in the humus layer (85 per cent of the total) than pine (45 per cent of the total). The highest density of mycorrhizal tips was up to $10/cm^3$ (MIKOLA *et al.* 1966). Root density may itself affect rates of infection at least during seedling establishment. Onions, which have a sparse root system, dit not become mycorrhizal during 10 weeks growth, whereas subterranean clover in the same field soil became heavily infected, as were two weed and two grass species in the field (BARROW *et al.* 1977). Many surveys of natural ecosystems reported 50-90 per cent of roots as being mycorrhizal. Sometimes certain plant species appear to be more heavily infected. READ *et al.* (1976) pointed out *Festuca ovina* as such a species. In a survey of mycorrhizal infection in plant species of a mixed deciduous forest *Fraxinus excelsior* and *Lonicera periclymenum* ranged from 90-100 per cent and 50-100 per cent, respectively but *Rubus vestitus* only had 28-53 per cent mycorrhizal roots. Most grasses in the tussock grasslands of New Zealand only contained about 30 per cent infection except in the subalpine scrub where it was higher (CRUSH 1973a). In pot experiments with *Lolium perenne*

I rarely found more than 30 per cent infection in a range of soils whereas tropical grasses such as *Brachiaria* sp. and *Paspalum notatum* commonly have 80-95 per cent mycorrhizal roots. Species differences have also been reported for crop plants. STRZEMSKA (1955) considered mycorrhiza to occur more rarely in rye than in wheat, barley, or oats, and also found infection differences in a range of legumes (STRZEMSKA 1975a). KRUCKELMANN (1975) found legumes and maize to be more strongly infected than potatoes. After prolonged monoculture potatoes also markedly reduced spore numbers in the soil and had some depressant effects on spore numbers in cropping sequences.

In general, mycorrhizal infection decreases in fertile soils and tends to be absent from garden soils, but field responses to added fertilizer have often been unpredictable (SHEMAKHANOVA 1967; MOSSE 1973a; STRZEMSKA 1975b; KRUCKELMANN 1975). A pot experiment cited by SHEMAKHANOVA (1967) illustrates the marked effects added nitrogen and phosphorus can have on mycorrhiza formation (Table 2).

TABLE 2. *Effects of P and N on mycorrhiza formation in* Pinus sylvestris *(after* SHEMAKHANOVA 1960*)*

| N mg/flask* | 7.9 | | | | 4.0 | | 2.9 | | 1.3 | |
|---|---|---|---|---|---|---|---|---|---|---|
| P mg/flask | 22.1 | 15.5 | 12.1 | 11.1 | 17.8 | 11.1 | 15.5 | 5.5 | 14.4 | 3.3 |
| Mycorrhizal tips/sdg | 2 | 3 | 0 | 0 | 12 | 23 | 3 | 7 | 0 | 0 |

* each flask contained 150 ml nutrient solution

In these experiments, as in some field observations on VA mycorrhizas (HAYMAN 1975), added nitrogen determined mycorrhizal frequency even more than added phosphate. THEODOROU & BOWEN (1969) studied the effects of nitrate and pH on colonization of pine roots and glass fibres. At pH values suitable for fungal growth, added nitrate reduced fungal growth along the roots but not along the fibres. Circumstantial evidence and studies on transplantation of seedlings raised in high and low phosphorus media suggested that phosphorus levels in the plant rather than those in the medium affect the establishment and disappearance of VA infection (MOSSE 1973b and unpublished data). SANDERS (1975) took this further by applying phosphorus via the leaves of mycorrhizal and non-mycorrhizal onions. Mean phosphorus inflow rates over the five-week period of foliar feeding were similar for both sets of plants, thus indicating that the fungus in the mycorrhizal plants had ceased to function. External mycelium of the fertilized plants did not increase further after three weeks

and at the end of the experiment weighed only half as much as that attached to unfertilized plants. This suggests that the absence of infection in fertile conditions is plant operated and depends on internal nutrient levels.

Taking into account results from many field and pot experiments as well as synthesis experiments with both VA and sheathing mycorrhizas (MOSSE & PHILLIPS 1971; MULLETTE 1976) one might construct a hypothetical response curve (Fig. 2)

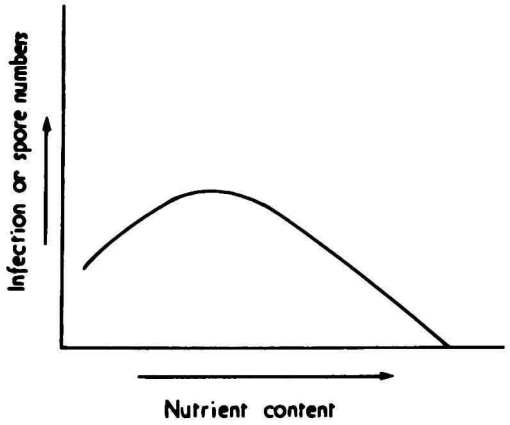



FIG. 2. *Effect of nutrient level on mycorrhizal infection*

relating mycorrhizal infection to nutrient addition. The turning point would depend on plant species. Such a curve might help to explain the divergent results reported in the literature because the starting point, i.e., the level of available soil P as well as amounts of nutrients added, would determine whether mycorrhizal frequency increased or decreased. Infection, then, is controlled by

a) Root density x soil infectivity,

b) Plant nutrient deficit = plant species x nutrient availability in the soil.

It is interesting that any pathogenic effects of VA mycorrhiza generally occur just before or at the time of decreasing infection (COOPER 1975; JOHNSON 1976; CRUSH 1976; MOSSE 1973b), when the plant is throwing off the invasion. The anatomical appearance of the infection also changes at that time.

Other factors determining mycorrhizal infection have been suggested, chiefly C:N ratio (HATCH 1937), light (PEYRONEL 1940; BOULLARD 1974; SHEMAKHANOVA 1967; JOHNSON 1976) and soluble sugar levels in the root (BJÖRKMAN 1942, 1970; HAYMAN 1974). Reactions to BJÖRKMAN's hypothesis have been reviewed by HACSKAYLO (1973) and put into perspective by LEWIS (1975). Infection in oaks was markedly reduced at 771 lux (SHEMAKHANOVA 1967) but with so little light

plant growth must have been affected in a variety of ways. In experiments with VA mycorrhiza, 13,000 lux reduced the dry weight of onions to one fifth of that after full light but infection only from 80 to 65 per cent (HAYMAN 1974). JOHNSON (1976) found rather complicated interactions between soil phosphate levels and shade in a range of plants. To some extent the phosphorus, nitrogen and sugar levels in plants are interrelated and depend not only on photosynthesis and external nutrient levels but also on plant growth rates and dry matter production. In practice, plant nutrient levels high enough to reduce or exclude mycorrhizal infection are only likely to occur in fertile agricultural soils, and plants from most natural ecosystems are likely to be on the upward slope of the response curve.

## 3. THE MYCORRHIZAL POTENTIAL

### 3.1. THE MECHANISM OF IMPROVED NUTRIENT UPTAKE

In the early literature growth effects of mycorrhiza are often attributed to a better utilisation of organic nitrogen compounds in humus. This is generally discounted at present (LUNDEBERG 1970). However, using $^{15}N$ labelling STRIBLEY & READ (1974) recently showed that the ericoid mycorrhiza of *Vaccinium* took up from the organic fraction nitrogen that was unavailable to non-mycorrhizal plants and to other soil fungi. After six months the mycorrhizal *Vaccinium* weighed 50 per cent more and contained 20 per cent more nitrogen per unit dry matter than the non-mycorrhizal. Mycorrhiza also increased nitrogen uptake from added ammonium sulphate at intermediate but not at high or low concentrations (STRIBLEY & READ 1976).

The effects of VA and sheathing mycorrhizas have mainly been explained on the basis of a better phosphorus supply. Recent studies on VA mycorrhiza have concentrated on the source of the extra phosphate and the role of the fungus in the soil, which has widened our understanding of how the system functions in its natural environment. The rapidly increasing mass of data concerned with plant growth responses to inoculation with VA endophytes has been well covered in recent reviews and the proceedings of a symposium. Their titles give an indication of the particular aspects covered. They are *Vescicular-arbuscular mycorrhiza* (GERDEMANN 1975), *Effects of vesicular-arbuscular mycorrhiza on higher plants* (TINKER 1975), *Microorganisms, the third dimension in phosphate nutrition and ecology* (BOWEN & BEVEGE 1977) and *The role of mycorrhiza in legume nutrition on marginal soils* (MOSSE 1977b). The proceedings of a symposium on *Endomycorrhizas* have also been published (SANDERS *et al.* 1975). Only the main points need be summarised here.

Most phosphate in soils is insoluble or strongly absorbed to soil particles. Up to 50 per cent may be present in organic form, and a third of that may be present as phytate. Only a small proportion, often less than 5 per cent of the

total soil P, is available to plants. In phosphate deficient soils the uptake of phosphate ions by plant roots exceeds the rate at which new ions move to the root surface and this leads to the development of a depletion zone, measurable in mm, around the roots. The depletion zone widens with root age as long as the root remains functional. Phosphorus uptake therefore depends primarily on the number of phosphate ions reaching the root surface, which in turn depends on their diffusion rate in the particular soil. Changes in root activity can only influence uptake if they result in the mobilization of otherwise insoluble phosphate.

Two mechanisms could account for the greatly increased phosphate uptake and growth of VA mycorrhizal plants that has been demonstrated in a range of experiments (Fig. 3).

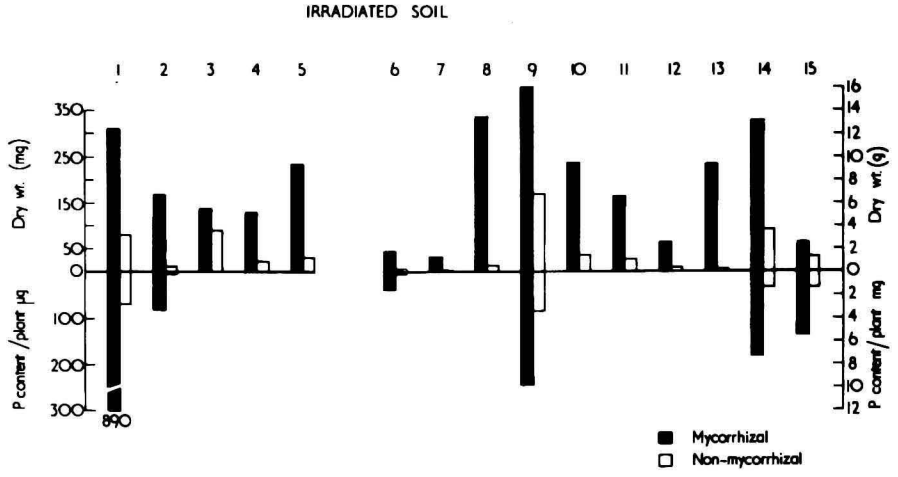



FIG. 3. *Effects of inoculation with VA endophytes on weight and phosphorus content of plants grown in sterilized soils.* 1. Allium cepa (HAYMAN & MOSSE 1971); 2. Lolium perenne (CRUSH 1973b); 3. Melinis minutifolia (*unpubl.*); 4. Paspalum notatum (*unpubl.*); 5. Stylosanthes guyanensis (*unpubl.*); 6. Brachypodium sylvaticum (*unpubl.*); 7. Centrosema pubescens (*unpubl.*); 8. Citrus (KLEINSCHMIDT & GERDEMANN 1972); 9. Fragaria *sp.* (HOLEVAS 1966); 10. Liquidambar styraciflua (*unpubl.*); 11. Liriodendron tulipifera (CLARK 1969); 12. Podocarpus totara (BAYLIS *et al.* 1963); 13. Vitis vinifera (POSSINGHAM & OBBINK 1971); 14. Zea mays (GERDEMANN 1964); 15. Glycine max (ROSS 1971)

Mycorrhiza could increase the effective absorbing surface of the root by means of the strategically situated network of hyphae that grow from the root surface and explore the soil beyond the depletion zone, or the fungus in the soil could mobilize -or induce the infected root to mobilize- insoluble phosphate unavailable to the non-mycorrhizal root. Soil labelling experiments with $^{32}P$ indicate that similar kinds of phosphate are taken up by VA mycorrhizal and non-mycorrhizal plants but that the former take up more, i.e., mycorrhizal plants do not mobilize insoluble soil phosphate. Nevertheless, many experiments have shown that mycorrhizal plants grow much better than non-mycorrhizal in soils enriched with such relatively insoluble phosphorus sources as apatite, bone meal, tricalcium phosphate, iron and aluminium phosphate and phytates. A more effective uptake of small amounts of soluble P associated with such phosphates is thought to explain this. It is not yet known whether sheathing mycorrhizas function in the same way.

Once taken up into the mycelium, phosphate is protected against further adsorption in the soil. Polyphosphate granules have been demonstrated in the fungi of both VA and sheathing mycorrhizas and are thought to be the form in which phosphate moves within the fungal system. Phosphate transfer from fungus to host is probably an active metabolic process that is not, or at least only partially dependent on breakdown of the arbuscule. The process of mycorrhizal uptake thus proceeds in three steps 1) uptake from the soil by the soil mycelium; 2) translocation from the mycelium in the soil to the mycelium in the root; and 3) transfer from the fungus to the plant. Any of these stages can be rate limiting but uptake from the soil is probably the most important one. Any factor affecting fungal spread in the soil such as pH, moisture content, aeration, temperature and interactions with other soil microorganisms will affect the uptake potential of the mycorrhizal system. The most important factor is probably the amount of phosphorus available to the fungus in the soil.

Some plants species only took up $^{32}P$ from labelled soils containing extremely little available phosphate when they were mycorrhizal.

In sheathing mycorrhiza the sheath may fulfill a storage function not only for nutrients taken up from the soil but also for those lost by efflux from the root.

Plant species differ markedly in their ability to grow in phosphorus deficient soils (Plate 1). Those with restricted root systems, short stubby roots and few root hairs (e.g. *Liriodendron*, onion and citrus) are generally less able to extract phosphorus and are therefore more dependent on mycorrhizal association than species with many root hairs, long fine roots and many root tips (e.g. *Gramineae*). Nevertheless even such species can benefit from mycorrhizas if soil phosphate is sufficiently low. Even in relatively fertile soils plants can benefit from mycorrhizas if growing conditions are good and rapid growth requires a high rate of phosphorus inflow. On the other hand,

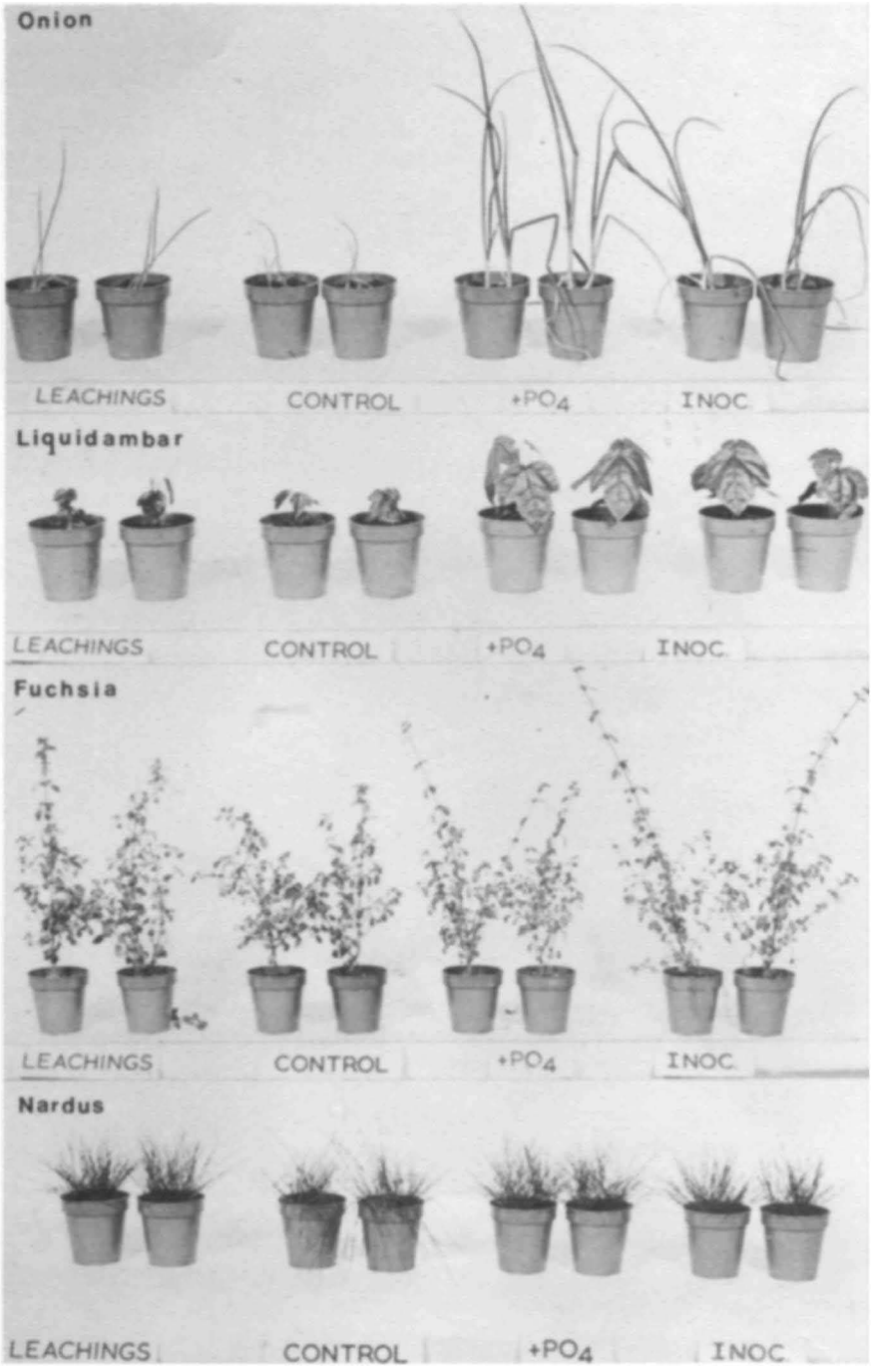



**PLATE 1.** *Response of different plant species, grown in the same soil, to calcium dihydrogen phosphate ($PO_4$) (100 mg P/kg soil), to inoculation with VA endophytes (inoc.), and to filtered washings (leachings) from the inoculum*

mycorrhizal plants can in some circumstances take up extra phosphate that is not reflected in extra growth.

Finally, mycorrhizal fungi differ in their capacity to aid nutrient uptake. This difference may depend on their adaptation to particular soils, perhaps on a tolerance of high levels of certain substances such as Al or NaCl, and reaction to physical soil conditions such as aeration, moisture content, and temperature. *In vitro*, in pots, and in the field, both VA and ecto-mycorrhizal fungi have been shown to differ in ability to utilize rock phosphate. However, in the same soil different VA endophytes used similarly labelled sources of soil phosphate. Sheathing mycorrhizas also differ in surface phosphatases and phytases.

The effect of mycorrhiza is therefore determined by plant species, fungal species and nutrient level in the soil.

The uptake of other ions can also be affected by mycorrhiza. Increased uptake of zinc (GILMORE 1971; BOWEN *et al.* 1974), potassium (POWELL 1975), strontium (JACKSON *et al.* 1973), and copper (MOSSE 1973a) have been reported.

## 3.2. QUANTITATIVE ASPECTS

Many interesting calculations have been made on fungal mass, the storage and translocating capacity of mycorrhizal systems, the spread of mycelium into soil, inter-root distances, and other factors of importance for the elucidation of mycorrhizal function and potential. It will be useful to bring some of them together here.

Mean inter-root distances in the top 10 cm of a 20 year old stand of *Pinus radiata* were 12.8 mm for long roots and 9 mm for short roots. In a 27 year old stand on another soil the values were 14.2 mm and 5.9 mm, respectively (BOWEN & THEODOROU 1967). Root length of *Gramineae* may be up to 50 $cm/cm^3$ of soil, which is twice that of legumes and other non-graminaceous herbs and 10-15 times that of woody plants (BARLEY 1970). PAVLYCHENKO (1942) recorded 53 cm root length/$cm^3$ soil in the top 10 cm of a wheat field in June. At 30 $cm/cm^3$ and a calculated inter-root distance of 1.8 mm there was no competition for phosphorus between wheat roots (NEWMAN & ANDREWS 1973). The mean distance between roots in a brown earth grassland at depths of 5, 10, and 15 cm was 0.39, 0.89, and 1.23 cm, respectively (SPARLING & TINKER 1975). Per unit length, clover roots including root hairs occupied one-fourth of the volume occupied by grass roots. Since inflow rates were one order of magnitude greater in the clover, phosphate depletion zones would also be greater (SPARLING 1976).

There was a constant relationship between VA fungus in roots and external media when $CaHPO_4$ was used as a phosphate source. This relationship no longer held, and relatively more external mycelium grew when Ca phytate was used as the phosphate source (MOSSE & PHILLIPS 1971). Furthermore, SANDERS & TINKER (1973) found a constant relationship between external mycelium and the length

of infected onion roots. Assuming a specific gravity of 1 for the hyphae, they calculated a length of 80 cm external hyphae/cm infected root. BEVEGE *et al.* (1975) gave the fresh weight of external hyphae as approximately 1 per cent of the total root weight in mycorrhizal clover, and MOSSE (1956) harvested 5 per cent from heavily infected apple rootlets. BURGES & NICHOLAS (1961) reported hyphal lengths of up to 6 $m/cm^3$ in the humus layer and up to 4 $m/cm^3$ in the $A_1$ horizon of a 60 year old pine stand in July. These amounts fell to 2.4 $m/cm^3$ and 1.3 $m/cm^3$, respectively, in September. These figures include live and dead hyphae and mycorrhiza as well as other fungi present. Mycelial strand growth of *Rhizopogon* varied widely with soil type and compaction reduced it greatly (SKINNER & BOWEN 1974a).

Translocation rates and distances covered by the external mycelium have been measured. Strands of *Rhizopogon luteus* conducted $^{32}P$ (applied at concentrations comparable to those in soil) towards mycorrhizal roots over distances of 1.2 cm in a pot experiment and 12 cm in the field and 30-80 per cent of the absorbed phosphorus was translocated (SKINNER & BOWEN 1974b). Within four days the external mycelium of mycorrhizal onion roots translocated into the plant appreciable amounts of $^{32}P$ applied 8 cm from the root surface. In the absence of mycorrhizas no $^{32}P$ reached the plant and radioactivity diffused in the soil over 1 cm (RHODES & GERDEMANN 1975). Very much lower diffusion rates to a root surface were measured by LEWIS & QUIRK (1967). In a soil given 100, 300, or 1,000 µg P/g soil, the velocity of phosphate ions was 0.04, 0.08, and 0.26 mm/day, respectively. BIELESKI (1973) calculated that in a VA mycorrhizal system having per mm root length four hyphae each 2 cm long and 25 µm in diamter, phosphate uptake could increase 60 fold if diffusion was limiting and 10 fold if uptake was proportional to surface area.

The number of entry points of the fungus into the root may have some importance for translocation since the movement of material from soil-based to root-based mycelium has to occur via these connecting points. The numbers reported in the literature range from 4-16/mm root length in juniper (LIHNELL 1939), 2.1-16.9/$mm^2$ root surface in strawberries and 4.6-10.7/mm root length in apples (MOSSE 1959), 0.6/mm root length in onion (SANDERS & TINKER 1973), 1.5/mm in *Festuca*, and 25-200/mm in *Calluna* (READ & STRIBLEY 1975). The number of entry points in *Calluna* is of an altogether different order of magnitude. This difference may be related to the different function of ericoid mycorrhizas; to make an impact on growth far greater quantities of nitrogenous substances than of phosphate would need to reach the plant.

The total mass of fungus associated with mycorrhizal roots is also of interest. Dissection of beech mycorrhizas indicated that 40 per cent of the total dry weight consisted of mantle. On the assumption that the feeding roots represent 10 per cent of total root mass something like 4 per cent of this would consist of fungus (HARLEY 1971). On the basis of a glucosamine assay HEPPER (1977) estimated that 4, 9 and 17 per cent of the dry weight of a

mycorrhizal root might consist of fungus in light, medium and heavily infected roots, respectively. Per gram weight, hyphae are several hundred times longer than roots and have the same total length as root hairs or a few times more. Therefore hyphae produce absorbing surface at much lower energy cost than roots (BOWEN & BEVEGE 1977).

## 3.3. OTHER EFFECTS OF MYCORRHIZA

### 3.3.1. Water uptake and longevity

It has repeatedly been suggested that mycorrhiza may help in the uptake of water and that mycorrhizal roots live longer. It is well known that phosphate deficient plants are more susceptible to drought (ATKINSON & DAVISON 1972) and it has been shown (SAFIR *et al.* 1971,1972) that the enhancement of water transport in mycorrhizal soya bean can be ascribed to a better phosphate nutrition. It is also well documented that soil fungi are able to survive much higher moisture tensions than plants and that they may therefore continue to take up nutrients when root hairs have collapsed. But because most mycorrhizas occur in the surface layer of soils and the water supply is obtained from the lower layers in times of drought, the more likely significance of mycorrhiza in such a situation is their continued ability to take up nutrients from relatively dry soil. Sheathing mycorrhizas in particular may act as a reservoir and as a protective layer against desiccation.
STRZEMSKA (1975a) suggests that in the *Gramineae* many non-mycorrhizal roots are deformed and presumably functional for shorter periods, but there are no confirmatory observations. Longevity is often stressed as an advantage of sheathing mycorrhizas. Although this may be advantageous for the uptake of nutrients other than phosphate, the chief advantage may be that such roots continue to support a network of easily replacable soil hyphae that are not subject to the same ageing process as roots in terms of suberization.

### 3.3.2. Antagonism to pathogens

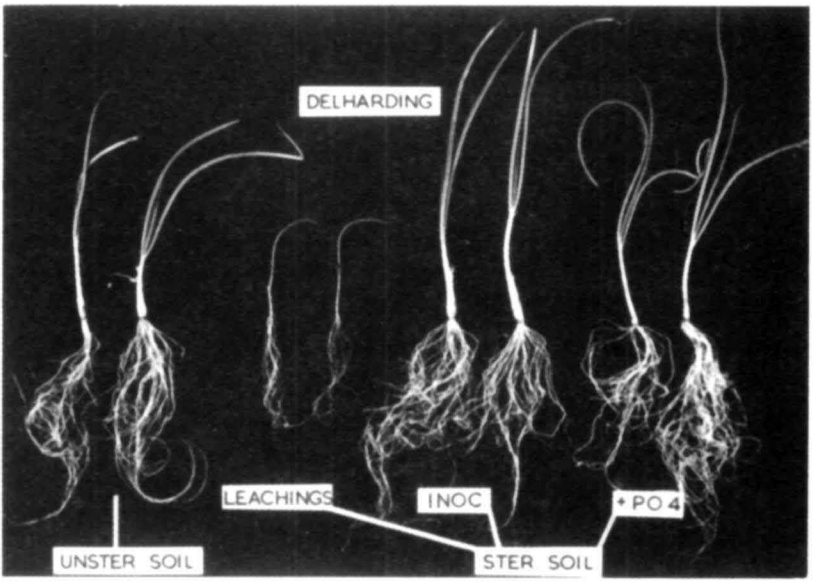
Field observations and laboratory results relating mycorrhizal infection to feeder root diseases have been well reviewed by MARX (1973). Although mycorrhizas never confer complete immunity, they often appear to reduce the severity of infection by other fungi or at least its symptom expression. MARX (1973) put forward several possibilities that might explain this: mechanical protection by the sheath, better nutrition of the plant, production of antibiotics by the mycorrhizal fungus, competition for infection sites, formation of phytoalexins by the plant (as in orchids) and changes in root exudates leading to a build up of protective rhizosphere organisms. To these may be added catabolite repression of degradative enzymes, proposed by LEWIS (1974) as a step towards mutualism. Evidence is accumulating that VA endophytes may exert similar effects. There is a competition for sites between endophytes and *Pyrenochaeta terrestris* in onions (BECKER 1976) and a reduction in

pathogenicity and in sporulation of *Thielaviopsis basicola* in tobacco (BALTRUSCHAT & SCHÖNBECK 1972). Symptom severity of *Fusarium* wilt is less in mycorrhizal tomatoes (DEHNE & SCHÖNBECK 1975), and there are instances of interactions reducing the population of pathogenic nematodes (SIKORA & SCHÖNBECK 1975). JANOS (1975) observed that mycorrhizal seedlings were more resistant to herbivory in a tropical forest. Nevertheless, it is by no means rare to find mycorrhizal infection in root lesions caused by other pathogenic fungi and some root rots have been ascribed, albeit erroneously, to mycorrhizal infection.

## 4. MYCORRHIZA IN THE NATURAL ECOSYSTEM

### 4.1. AGRICULTURE, PASTURE AND FOREST

Even though we have some knowledge and appreciation of mycorrhizal potential, a quantitative assessment of the mycorrhizal contribution to nutrient uptake in an undisturbed ecosystem presents many difficulties,chiefly because these are dynamic systems. Nutrient requirements vary both during the annual growth cycle and, for perennials, during their life span. The possible significance of mycorrhizas is linked to these fluctuating needs. In annual crops an adequate P supply is particularly critical during early growth when root density is low and depletion zones do not yet overlap. Because phosphate is removed by the crop and high yields are usually desired, most annual crops are grown with some fertilizer input. This addition would have to be larger if there were no mycorrhizas. COOKE (1965) stated that in general 25 per cent of applied phosphate is taken up by the crop in the first year and the rest reverts to unavailable forms unless a reserve of potentially available P has been built up over the years by repeated fertilizer application. Many wheat growing soils in Australia are so P deficient and have such high fixation rates that the yield is directly proportional to fertilizer P input. Even in Danish agricultural soils with a long history of generous fertilizer application, further phosphate addition became necessary to maintain high productivity when no phosphate had been given for two years (LARSEN 1976). The only question is the extent to which mycorrhizal infection is suppressed by heavy fertilization under agricultural conditions. Plate 2 shows the effect of removing VA endophytes from an agricultural soil at Rothamsted. Where poor growth occurs after soil sterilization, particularly of a relatively mild kind such as steaming, low dosage irradiation (below 1 Mrad), or fumigation, one suspects that this is due to lack of mycorrhizas. It sometimes occurs in nurseries and has been overcome by re-inoculation with VA endophytes (KLEINSCHMIDT & GERDEMANN 1972; HATTINGH & GERDEMANN 1975). In the past, poor growth after soil sterilization was often attributed to soil toxicity. The typical response to toxicity is initially poor growth that improves as a microbial population




By courtesy of D.S. Hayman

PLATE 2. *Growth of onions in a Rothamsted soil. Plants in the unsterile soil and those labelled 'inoc.' are mycorrhizal; 'leachings' and '+$PO_4$' plants are without mycorrhiza.*
*$PO_4$ = calcium dihydrogen phosphate, 100 mg P/kg soil*

re-established itself and detoxifies the soil. Poor growth due to lack of mycorrhiza proceeds in the opposite way, good initial growth while the seed reserves last, followed by a gradual decline as nutrients run out.

In forests, only a small proportion of the annual P requirement (less than 2 per cent in a 20 year old pine stand (SWITZER & NELSON 1972) comes from the soil. The extreme phosphorus deficiency in soils under luxurious tropical forest in the Amazon basin shows that in such situations nutrient cycling is very tight. Of the annual phosphorus requirement sixty to eighty per cent may be recycled within the plant and the balance taken up again directly from the decaying litter without ever reaching the soil. The function of mycorrhiza in such a system could be twofold. The fungi could help to accelerate the cycle by assisting in litter breakdown and by acting as a direct link for transferring nutrients from the litter into the plant. They might also act, as in the soil, as an extension of root absorbing surface and, in the case of sheathing mycorrhiza, as a temporary storage tissue during flushes of nutrient release. Fresh pine litter contains 1 per cent total P of which approximately 20 per cent is inorganic and 20 per cent is phytate (BOWEN & THEODOROU 1967). Mycorrhizal fungi in culture can utilize phytate (THEODOROU 1968; SHEMAKHANOVA 1967) but so can sterile plants. The mycelium and rhizomorphs often seen in

litter usually belong to saprophytes, fungi such as *Mucor, Mortierella* and *Penicillium* (WENT 1971) which are not mycorrhiza formers. GADGIL & GADGIL (1971) reported that litter decomposition actually appeared to be retarded by mycorrhizal fungi and MACAULEY (1975) concluded that while fungi released P from litter they retarded the mineralization of N.

The important effects of mycorrhiza on the establishment and early growth of seedling trees planted in the field is well illustrated by Russian work in which pure cultures of ectomycorrhizal fungi were used as inoculum. SHEMAKHANOVA (1967) cited many instances of better survival (30-80 per cent in 2-year-old pines, 2-36 per cent in 3-year-old oaks) and of increased dry weight (0-131 per cent and 25-130 per cent in pine seedlings and up to 140 per cent in oak) according to soil and site. Inoculation sometimes caused small growth depressions. The average diameter of oaks was increased by up to 25 per cent in a 9-year-old oak stand. General experience in forestry has shown that initial advantages in early growth persist in the mature stand.

Grasslands resemble forests in that phosphorus moves to the roots during winter, but they resemble agricultural systems which are subject to a net loss of nutrients due to grazing followed by removal of the animals. CRUSH (1973a), SPARLING (1976) and KOUCHEKI & READ (1976) who studied inoculation responses of grasses in upland and tussock grassland soils, concluded that despite abundant infection at these sites the precise role of mycorrhiza was difficult to interpret and of doubtful significance. One difficulty encountered was that considerable release of nutrients occurred when these high organic soils were sterilized. Therefore, no growth responses were observed until some time after inoculation, i.e., four months in the investigations of KOUCHEKI & READ (1976) and twelve months in one of the three soils studied by SPARLING (1976). By contrast clover in all three soils showed very large responses to inoculation. CRUSH (1973a) found that out of five grass species tested only two benefitted from inoculation and then only in soils at high altitudes which contained less than 8 ppm-Truog soluble P. Growth of the other species was slightly depressed by infection. CRUSH thought that the above effects, also observed by MAGROU (1938) and MOSER (1963), might be explained by the slower mineralization of phosphate at high altitudes.

The need for soil sterilization, arising from the universality of VA endophytes, is not the only factor that makes interpolation from pot experiments to field situations difficult. A short account of an attempt to assess the involvement of V' corrhiza in phosphate uptake in a mixed deciduous forest in England w. .l illustrate some of the other problems.

## 4.2. THE ROLE OF MYCORRHIZA IN PHOSPHATE UPTAKE AT MEATHOP WOOD IBP SITE

Species included in this study were *Fragaria vesca, Viola riviniana, Brachypodium sylvestris, Rubus vestitus, Fraxinus excelsior* and *Betula pubescens*. Preliminary experiments (Plate 3) with the grass *Melinis*


PLATE 3. Melinis minutifolia *in irradiated Meathop Wood soil*
*P = $KH_2PO_4$, 100 mg P/pot; N = $NH_4NO_3$, 200 mg N/pot*

*minutifolia*, a species very efficient in phosphorus uptake, showed that even for this species phosphorus was growth limiting in the soil but when phosphate had been added there was also a response to nitrogen. Inoculation experiments in the irradiated soil (Table 3) showed that growth of five locally common species was greatly improved by inoculation with the indigenous mycorrhizal fungi.

TABLE 3. *Dry weight (mg) of plants with and without mycorrhiza*

| Plant | Inoculated with indigenous fungi | Non-inoculated |
|---|---|---|
| *Brachypodium* | 453 | 15 |
| *Viola* | 349 | 146 |
| *Rubus** | 2756 | 1122 |
| *Fraxinus*** | 174 | 125 |
| *Betula* | 1718 | 176 |

* including weight of original cutting

** excluding weight of original cutting

The addition of monocalcium phosphate at the rate of 100 mg P/kg soil produced even better growth responses except in *Brachypodium*. Inoculation responses in irradiated soil are frequently better than in unsterilized soil and this was also the case here (Table 4; Plate 4).

TABLE 4. *Dry weight (DW) and P uptake (P) of inoculated plants in irradiated (I) and unsterlized (U) soil*

| Plant | Soil | DW (mg) | P (µg) |
|---|---|---|---|
| *Viola* | I | 184 | 403 |
| | U | 91 | 156 |
| *Fragaria* | I | 1124 | 1253 |
| | U | 549 | 410 |
| *Fraxinus** | I | 160 | 470 |
| | U | 44 | 241 |
| *Betula* | I | 160 | 319 |
| | U | 88 | 190 |

* weight and P gain of cuttings from one year old seedlings

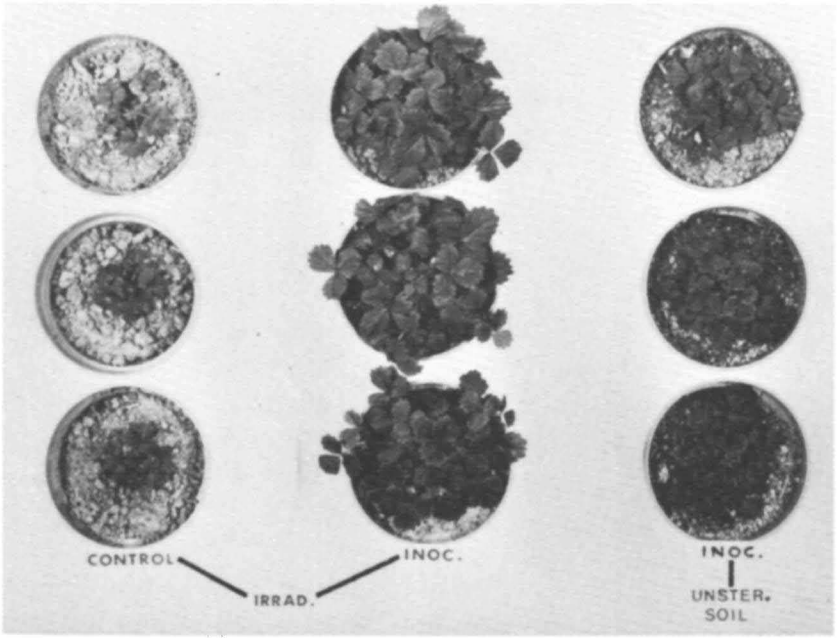



PLATE 4. *Inoculated and non-inoculated* Fragaria vesca *in unsterile and irradiated Meathop Wood soil*

That soil-available phosphorus was little changed by the irradiation treatment was shown by chemical analysis and also by the early growth of strawberry seedlings (Table 5).

TABLE 5. *Dry weight (DW) and mycorrhizal infection of* Fragaria *seedlings in irradiated and unsterlized soil*

| Treatment | 3 weeks | | 5 weeks | |
|---|---|---|---|---|
| | DW(mg) | Infection (%) | DW(mg) | Infection (%) |
| Irradiated soil | 22 | 0 | 28 | 0 |
| Unsterilized soil | 22 | 0 | 35 | 30 |

Their growth was equally good in irradiated and unsterlized soils until the seedlings in the unsterilized soil became mycorrhizal, after which they grew better. It was therefore decided to compare non-mycorrhizal plants (NM) in irradiated soil with inoculated plants (M) in unsterilized soil. This would, if anything, give an advantage to the non-mycorrhizal plants. Indigenous mycorrhizal fungi were used as inoculum. Results are shown in Table 6.

TABLE 6. *Dry weight (DW) and P content (P) of inoculated plants in unsterilized soil (M) and non-inoculated plants in irradiated soil (NM)*

| Plant | DW(mg) | | P(µg) | |
|---|---|---|---|---|
| | M | NM | M | NM |
| *Brachypodium* | 355 | 38 | 182 | 18 |
| *Viola* | 142 | 22 | 157 | 22 |
| *Fragaria* | 214 | 47 | 165 | 37 |
| *Fraxinus** | 173 | 125 | 304 | 95 |
| *Rubus*** | 1115 | 1122 | 800 | 394 |

* gains made by cuttings

** total weight and P content of leaf-bud cuttings

The difference between M and NM plants, although originally induced by the inoculation treatment, cannot be attributed solely to fungal uptake. As the mycorrhiza improved plant growth, the plants themselves developed larger root systems which would also contribute to greater nutrient uptake. Small phosphate starved plants sometime have abnormally high phosphate concentrations. When therefore adjustments were made to allow for the larger size of M roots on the basis of P content and weight of the NM roots, the calculations often showed a very small or even negative involvement of mycorrhiza in P uptake. This was obviously absurd because inoculation had induced much better growth. Perhaps a better measure of mycorrhizal involvement would be to determine the size of phosphorus application necessary to produce plants as large as the inoculated ones. The best solution would be to find a systematic fungicide that would inhibit fungal uptake *in situ*, but this is likely to be difficult because few systemics act against Phycomycetes and most are translocated upwards and often are relatively insoluble. In a preliminary study of this problem Benomyl added to soil inhibited mycorrhizal infection (BOATMAN *et al.* 1978). This was also reported by BERTOLDI *et al.* (1977).

Another aspect that emerged during our investigations indicates even more strongly that *in situ* inhibition of fungal uptake is the best approach. When soil was collected for the experiments the litter layer was removed. This contained four times as much $NaHCO_3$-soluble P as the soil below it. If this layer had not been removed but mixed with the soil it would have added only 1.5 per cent extra available P, but *in situ*, as a top layer, it had very marked effects on seedling growth. The soil profile and the thickness of the litter layer were found to be highly variable in the wood. We therefore compared results of inoculation in three types of reconstructed profiles similar to those found in the wood. Table 7 shows the results obtained.

TABLE 7. *Dry weight (mg) of mycorrhizal (M) and non-mycorrhizal (NM) plants in soil reconstructed in its natural profile. Litter depth decreased from profile 1 to profile 3*

| Plant | Profiles | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Subsoil | | 1 | | 2 | | 3 | |
| | NM | M | NM | M | NM | M | NM | M |
| *Fragaria* | 29 | 143 | 1141 | 385 | 13 | 263 | | |
| *Brachypodium* | 32 | 28 | 1133 | 604 | 174 | 469 | 43 | 49 |
| *Viola* | | | | | | | 22 | 138 |
| *Rubus* seedlings | | | | | 144 | 509 | | |
| stem cuttings | | | | | 819 | 735 | | |

M = inoculated plants grown in unsterilized soil
NM = non-inoculated plants grown in irridiated soil

Profile 2 was considered to represent the most common type in the wood. In profile 1 litter occupied more than half the pot. It is likely that the exceptionally good growth of the NM plants in this profile was due to nutrient release following sterilization. The comparable M plants were grown in unsterilized soil probably containing less available P. The potential pathogenicity of mycorrhizal infection may also have found expression in this relatively fertile soil where plants generally grew much better. It is evident that considerable practical difficulties will be encountered in any attempt to make a quantitative assessment of mycorrhizal significance in such a variable environment.

The investigation suggested one further conclusion, namely that mycorrhiza might be particularly important in early seedling establishment. In profile 2 (Table 7) *Rubus* seedlings benefitted from inoculation but stem cuttings, which had an initially higher P reserve, dit not. Practical experience with forest trees has already established the importance of mycorrhiza for seedling development and the extremely small size of orchid seed and lack of seed reserves has always been regarded as a probable explanation for their mycorrhiza dependence. The mycorrhizal *Rubus* cuttings were marginally larger and contained 20 per cent more P after 6 weeks but after 12 weeks (Table 7) infection had reduced growth. *Rubus* has a very extensive root system with many long root hairs. It grew vigorously, and in small pots this resulted in great root density. It is noteworthy that in the survey of Meathop Wood plants *Rubus* had the lowest infection level, which is probably an indication of the self-adjusting character of VA infection.

## 4.3. SPECIAL SITUATIONS

In ecological studies the possibility of species interactions always attracts attention. On the basis of results obtained by WOODS & BROCK (1964) and BJÖRKMAN (1960) it is occasionally suggested that movement of nutrients could occur both between individuals and also between plant species via common mycorrhizal fungi. Although one frequently sees connections between roots of the same species one rarely finds interspecies connections. Since infection can spread from one species to another some links must occur. The orchid studies of BJÖRKMAN (1964) are a special case, and the interspecies transfer of $^{32}P$ and $^{45}Ca$ reported by WOODS & BROCK (1964) could have occurred in many ways. Much more likely and interesting for mycorrhizal studies is the question of interspecies competition. STONE (1949) showed that ectomycorrhizal Monterey pine competed successfully with Sudan grass for poorly soluble P and obtained a relatively large share of a limited supply when it was mycorrhizal. A similar situation probably exists between grasses and clovers or other pasture legumes. SPARLING (1976) showed that clovers had about half as much root length per unit weight as grasses and without mycorrhiza grew very badly in soils where grasses grew quite well. In mixed swards clover is much more

likely to become established and to persists if it is mycorrhizal.

In phosphate deficient soils mycorrhizas are potentially important for the proper functioning of symbiotic nitrogen fixation by rhizobia. This has been demonstrated in sterilized (MOSSE *et al.* 1976; SMITH & DAFT 1977) and unsterilized soils (MOSSE 1977a); the subject has been reviewed by MOSSE (1977b). Mycorrhizas enable the plant to take up the phosphorus necessary for successful nodulation. They may also interact in other ways with rhizobia, but this has not yet been proved. Mycorrhizas also occur in non-leguminous plants with nitrogen fixing nodules. A combination of the two symbiotic systems offers great advantage to pioneer plants on reclaimed waste land and coal spoils (DAFT & NICOLSON 1974; DAFT *et al.* 1975; DAFT & HACSKAYLO 1976). Trees with sheathing mycorrhizas formed by *Pisolithus tinctora* are also good colonizers of such sites since the fungus develops prolific mycorrhizas with pine at soil temperatures ranging from 19 to 47$^{o}$C (MARX & BRYAN 1975). High soil temperatures, low pH and sometimes heavy metal toxicites, are particular obstacles to the colonization of such sites.

VA endophytes are also very effective in the aggregation of dune sands (KOSKE *et al.* 1975; SUTTON & SHEPPARD 1976). They increased aggregate weight from 0.9 to 2.5 g per kg dry soil and to 127 g after a second crop. Although other soil fungi were present, mycelium of VA endophytes predominated in the aggregates. NICOLSON (1960) considered heavy mycorrhizal infection as a developmental stage in the colonization of dune sands. If the fungi have special binding power they may also have a function in erosion control.

Many possibilities and many problems remain in mycorrhiza research. Experimental techniques are available to study particular problems but results must be treated with caution when one tries to relate them to natural situations. The potential value of myccorhiza has been clearly demonstrated but how far this can be utilized in crop production and to what extent it may be endangered by new agricultural and forestry practices remains to be determined.

## 5. ACKNOWLEDGEMENTS

The work at Meathop Wood was done in conjunction with Dr. D.S. Hayman. I would like to thank the International Biological Programme for a grant towards the Meathop Wood investigation and I am indebted to Mr. D. Arnold and Mr. D. Paget who did much of the work.

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## 7. DISCUSSION

LEVIN (Texas): Is there a relationship between the likelihood of the occurrence of infection on the one hand and the ability of species to obtain nutrients on the other hand? In other words, are plants which are poor at obtaining nutrients more likely to have mycorrhiza than plants that are better adapted for obtaining nutrients?

MOSSE: I don't think there is any evidence that this is so. You cannot make any categorical statement. It all depends on the type of soil, on the soil fertility, and above all on the phosphorus levels in the plant.

LEVIN: I was curious as to whether there are any biochemical preadaptations in different species which might cause some to be more likely than others to form mycorrhizal associations.

MOSSE: I think that all these things are possible, and we will know as soon as people go into it much further. But at the moment we are still at a very early stage. We are just learning to manage our experimental system and we are just beginning to formulate the problems. There are so many snags. I don't doubt there will be interactions of the kind you suggested, but they will be minor.

VAN DEN ANDEL (Amsterdam): Is there an effect of mycorrhiza on the reproductive behaviour of plants? You only talked about the effects on growth.

MOSSE: There is some work which suggests that in pot experiments mycorrhizal plants flower earlier. The suggestion has been made that this might be an hormonal effect. But I think it is probably also a nutritional effect.

VAN DER AART (Oostvoorne): You mentioned that there are some plant families without mycorrhiza, for instance *Carex*. How can these species compete with species with mycorrhiza in vegetations on soils which are low in phosphates? Is anything known about how they get their phosphates?

MOSSE: This question has been investigated, but no definite conclusion was possible. It has something to do with growth rates. Some plants have higher phosphorus concentrations, and some can grow with lower phosphorus inputs than others can. It also depends on the species they are competing with. Another thing is that *Carex* species often occur on waterlogged soils. VA mycorrhizas do not flourish under waterlogged conditions. There also are some reports that *Carex* species sometimes possess VA mycorrhiza. It is unusual, but seemingly it can happen.

ANONYMOUS : You said tropical grasses show a higher infection rate of

mycorrhiza than temperate grasses. Tropical grasses are most common in savannahs and woodlands were there is a strong seasonality of growth. Could it be that the rate of mycorrhiza infection is higher in all types of plants which have strong seasonality? And my second question is: can tropical grasses stand a higher infection rate of mycorrhiza than temperate grasses before it become pathogenic?

MOSSE: As to your last question, it does not become pathogenic because the infection rate is too high. It is pathogenic under circumstances where there is no growth response to extra phosphate. Then the mycorrhiza still brings in extra phosphorus, but it does not produce extra growth. The advantage of the plant-microorganism system is no longer obvious in terms of growth. At such supraoptimal phosphorus levels, the disadvantages to the plants from any fungal attack prevail. As to your question on seasonality, no one seems to have worked on it.

GIGON (Zürich): Do you have any idea of the importance of mycorrhiza in heavy-metal soils, which are rich in zinc, chromium, and nickel?

MOSSE: It is known that mycorrhiza may help in zinc uptake in zinc-deficient soils. But what happens in these abnormal soils is anybody's guess.

GRIME (Sheffield): Does the mycorrhiza system, particularly in ectotrophic evergreen species, make it possible to exploit soil in which nutrients, such as phosphorus, are only available for brief periods during the year at low concentrations.

MOSSE: This is a question of storage capacity, i.e., the volume of mycorrhizal tissue. In ectotrophic mycorrhiza the total volume is about 4 per cent of that of the total root system. Although it may contain poly-phosphate granules, these are not large amounts. In VA mycorrhiza the volume is between 4 and 17 per cent of the fine roots only. But in terms of energy the mycorrhiza is very much more efficient in making absorbing surface than the roots themselves. And it moves its cytoplasm around. So it is a much more mobile system.

GRIME: Do I interpret you correctly, is the mycorrhizal plant getting a root system at minimal synthetic cost?

MOSSE: Absolutely. There are figures that are fantastic. It does not lose anything when moving around in the soil, and the whole system is interconnected. So it can explore very large areas of soil, where the roots would never come. It is a very mobile system. The mycorrhiza has evolved over long periods of time as a beautiful system.