Mycorrhizas: The Present Position

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Abstract

THE current state of research on mycorrhizas is reviewed, with special emphasis on vesicular-arbuscular mycorrhizas. There has been little advance in the taxonomy or genetics of these fungi recently, though this is urgently needed. Their ecology is in a confused state, with large amounts of information but few major systematic studies of particular topics, so that it is difficult to make generalizations, and mathematical modelling methods are recommended to help in the derivation of general principles.

Interactions with the host via nutrition are quite well understood; there are other suggestions relating to host carbon loss, which seem very probable, and to effects on the host water status or hormone balance, for which there is less evidence. Responses due to improvement in phosphorus nutrition continue to be by far the most important, and possible practical applications are discussed.

THE expansion of work on mycorrhizas in the past decade has been explosive, especially for the vesicular-arbuscular mycorrhizas (VAM). It is now impossible to review the whole subject in a single paper; the following reviews and general papers, published recently, provide useful information: Marks and Kozlowski (1973); Tinker (1975a); Sanders *et al.* (1975); Gerdemann (1975); Hayman (1979); Tinker (1978); Rhodes and Gerdemann (1980); Mosse *et al.* (1981); Hayman (1981).

Biology and Taxonomy

No significant advances have taken place in this subject for some time, though this is probably where they are most urgently needed. The major aim of growing the VA endophytes in single-member culture has still not been achieved, though two-member cultures have been established in solution culture and in tissue culture (Elmes and Mosse 1980). Further, there is lack of information on the reproductive processes of the fungi and it is still not known whether or not there is any sexual reproduction. No work on their genetics seems to have been reported so far. New endophytes continue to be discovered, including interesting species such as *Glomus epigeus* (Daniels and Trappe 1979), but the best yield responses continue to be produced largely by the well-established endophytes such as *Glomus mosseae* and *Glomus fasciculatus.* Mosse *et al.* (1981) gave a complete list of all the reports of new

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endophytes to date, and raised serious questions over the validity or value of some of the new species identifications. They noted that it is very easy to find spores with minor variation from the existing descriptions; therefore, new species should only be named when the range of variation of taxonomic properties in its spores has been established. No evidence has appeared so far indicating that new strains with remarkable yield-enhancing properties are likely to be discovered, and the present situation continues to emphasize the severe disadvantages of being solely dependent upon prospecting for new material, with no possibility of using sexual recombination as a source of variation. There is new evidence for intra-specific variation from various sources: Abbott and Robson (1978) showed that isolates of *Glomus* from two different sites gave different yield responses; Gildon and Tinker (1981) found that isolates of *Glomus mosseae* isolated from an area heavily contaminated by zinc and cadmium had developed a greater resistance to these metals than the normal endophyte; and Lambert *et al.* (1980) detected differences in ability of different isolates to grow on acid soils. There is consequently considerable genetic diversity, and great scope for new developments if the normal techniques of breeding become available.

Progress with the ectomycorrhizas (ECM) should be more rapid, in that the fungi are more specific for hosts, there are already well-documented cases of practical economic benefit, and for at least some of the fungi normal sexual propagation can be effected. The major problem here seems to be the very complex ecology, with several different fungi forming mycorrhizas in succession as the plant grows older (Foster and Marks 1967). Certain species of the ectotrophic mycorrhizas such as *Pisolithus tinctorium* have been selected for their large potential advantage to the host (Marx 1977).

Ecology

Effect of Environment

Our knowledge of the ecology of the mycorrhizal fungi has recently been summarized fully by Mosse *et al.* (1981), who concluded that low light levels usually reduce infection, in line with the original Bjorkman hypothesis of the importance of soluble carbohydrates in the root as a nutrient for the fungus. Daft and El Giamni (1978) noted that defoliation had the same effect on VAM as low light levels. There are some observations of the opposite effect, but presumably this is a question of the complex balance of the growth rates of the two organisms. The effects of this demand for host carbon is discussed later.

In many conditions light intensity and temperature may change together, and it is very certain that temperature affects mycorrhizal development greatly; in general mycorrhizal fungi prefer higher temperatures than those experienced by most temperate crops. ECM fungi appear to grow best around 20°C in single culture, and the *Pisolithus* mycorrhiza can develop in particularly high temperatures (Marx *et al.* 1970). There is much information on the uptake of phosphorus, nitrogen (as ammonium) and potassium by the fungal sheaths of beech mycorrhizas, with the temperature optimum usually lying above 25° C for the first two elements, but below 20° C for potassium (see Harley 1969, for a full discussion). VAM appear to develop most rapidly at 16° C or above (Smith and Bowen 1979), and a physiological basis for this has been discovered in the rapid decrease in translocation rate of phosphorus in the hyphae below 15° C (Cooper and Tinker 1981), which implies that the translocation rate of carbon compounds is similarly affected. There is much evidence that different mycorrhizal fungi are adapted to different temperature regimes, and that even different isolates of the same *Glomus* species can differ (Schenk *et al.* 1975). Further investigation of this is highly desirable, especially in view of the suggestion of Black and Tinker (1979) that low soil temperatures may delay the establishment of useful levels of infection in temperate annual crops until the main uptake period for P is passed. This sensitivity to low temperatures is presumably a direct effect on the growth rate of the fungus, because roots at low temperature generally have high concentrations of soluble carbohydrates, which should be an advantage for infection, and the slower growth of the root system would normally allow the fungus to establish a higher percent infection.

There is general agreement that excess water, low oxygen levels and reducing conditions inhibit mycorrhiza formation, but the precise mechanisms are not clear, and there does not seem to be any major practical need for the question to be pursued. Skinner and Bowen (1974) measured the rate of extension of mycelial strands of *Rhizopogen* mycorrhizas with *Pinus radiata* into soil, and found large differences between soils, and up to 80% reduction caused by soil compaction, possibly due to poor aeration. It appears far more important to determine the responses of mycorrhizas to dry conditions, and whether they still enhance plant growth under these conditions. Both major forms of mycorrhiza appear to tolerate dry soils in that, even if mycorrhizal fine roots are killed off, new roots formed when water is re-supplied are rapidly re-infected, and VAM occur in quite arid environments (e.g. Reeves *et al.* 1979). The general impression that mycorrhizal development occurs most rapidly at intermediate moisture tension has been confirmed by direct experiment by Reid and Bowen (1979), showing most infection at 0.19 MPa. Reid (1979) has summarized much other work on the ECM.

It is quite certain that, in controlled single experiments, adding phosphorus decreases infection percentages for VAM, and that adding nitrogen reduces ECM and possibly VAM infection. It is also certain that it is the internal level of P in the root that causes the reduction in infection by VAM possibly via an effect on the integrity of the cell membranes (Ratnayake *et al.* 1978). However, the inference which might be drawn from this — that infection is always less in more fertile soils—is not necessarily true. At least two general surveys of infection (Hayman *et al.* 1976; Black and Tinker 1979) have shown little or no connection between percent infection by VAM and the fertility of the soil as measured by soil analysis, and strong infection with ECM has been noted on heavily fertilized soils (Le Tacon and Valdenaire 1980). The effect of adding P may also be shortlived, which suggests a rapid adaptation by a heterogeneous fungal population to additions of P (Sparling and Tinker 1978a). This and equivalent results which imply genetic diversity has started a search for P-tolerant mycorrhizal fungi; though Porter *et al.* (1978) found such evidence on high-phosphate field plots, Jasper *et al.* (1979) detected differences in P-tolerance between VAM populations on virgin and fertilized soils. This clearly needs more investigation, if we desire to have fungi which can be inoculated into crops growing under moderately fertile conditions, since mycorrhizal infection is of little benefit if it only gives yield responses under conditions where the best yield is far below that obtainable with large dressings of phosphorus fertilizer. However, it should be borne in mind that mere tolerance of moderate levels of phosphorus is not sufficient; there must also be an adequate rate of spread, and ability to benefit the host plant under these conditions.

Effects of pH have been frequently noted (Graw 1979) but, in general, good pH tolerance exists. It is difficult to separate effects on the host plant, or the physico-chemical changes in soil nutrient availability, from direct effects of the soil acidity on the fungal growth or spore germination. Apart from a consensus that *Glomus* species favour neutral and alkaline soil, whereas *Acaulospora* and *Gigaspora* species are more tolerant of acidity, no generalizations seem possible (Mosse 1973; Mosse *et al.* 1981).

The subject of tolerance to heavy metal pollutants has attracted an interest, because polluted sites are often reclaimed land, and as such may be expected to give scope for artificial inoculations (see Marx *et al.* 1978 and references quoted by them). There is no doubt that metals do inhibit growth and development of both ecto- and endo-mycorrhizal fungi but the discovery of Cd and Zn tolerant strains of *Glomus mosseae* on old mine spoil (Gildon and Tinker 1981) raises the possibility that this may in practice be less important than expected.

Models of Fungus Spread

Comparisons between hosts or between fungi are often made by simply infecting plants in an arbitrarily chosen soil, growing them in a greenhouse under non-standard conditions, and then carrying out a single harvest at some arbitrarily chosen time. However, these processes are complex, even under identical soil and environmental conditions, because it is difficult to present inoculum in precisely standard conditions, and even more so because the system is highly dynamic and interactive, with both root and fungus growing at the same time, and mutually influencing each other's growth rate. Such simple comparisons are therefore probably incomplete and may be misleading. It is almost invariably found, where sequential measurements are made, that as the root system develops from a seedling, the percentage infection remains low at first, then rises sharply and usually levels off into a plateau (see Black and Tinker 1979). If comparisons are made of hosts, endophytes or soil conditions at a single harvest, the results may depend greatly upon when this is made. In the broadest sense, there are so many interactive feedbacks in a mycorrhizal plant that modelling appears almost essential to separate out the important and fundamental variables and parameters from merely fortuitous relationships. The simple model proposed by Tinker (1975a, b) takes account of only one of these interactions, namely, growth of the host on degree of infection, in that it related the rate of development of new infections to the amount of uninfected root present at that time. This equation attempted to express the underlying factors by the two parameters — one a "susceptibility" or "infectability" of the host-endophyte combination in these conditions, and the second a measure of the "plateau" level of infection. The fact that this "plateau" level is always less than 100%, and often much less, is rather surprising, and has never been properly explained. There is no obvious reason why all root should not eventually become infected; perhaps this is most striking in measurements of dense, heavily infected perennial root systems, where the inoculum potential must be extremely large, but where infection consistently remained around or below 50% (Read *et al.* 1976; Sparling and Tinker 1978a). It appears to be species-dependent (Warner 1980), endophyte-dependent (Sanders *et al.* 1977) and probably dependent upon soil conditions, though no sufficiently exact comparisons seem to be available here.

We have recently found (Buwalda, Ross, Stribley and Tinker, in preparation) that a version of the Lotka-Volterra equation gives a much better fit to more exact data, and allows the rate of development of infection to be described with just these two parameters, and a knowledge of the way in which root density is increasing. When development of this and other types (Smith and Walker, private communication) are completed, it may be possible to compare endophyte-host-environment relationships in a more exact and meaningful fashion. More elaborate models which take into account the interaction of mycorrhizal infection on the percent P in the host, and hence on its growth rate and on future infection levels, have been constructed (Sanders, personal communication). Finally, if the demand for carbon by the fungal symboint is sufficiently large for it to affect the host, this also will have to be built into a more complete model.

Interactions with Other Organisms

This topic is in a greatly confused state, with a variety of largely isolated observations, and almost no useful generalizations which can be made (Mosse *et al.* 1981). Thus different bacteria can depress, increase or have no detectable effects on colonization by ECM, and the effects differ *in vitro* and on mycorrhizas. One suspects that a change in soil conditions might well also affect any such results, and it is exceedingly important that studies should be done on such a scale, with a wide range of organisms and conditions, that we can know whether dependable general rules can be formulated. This is so important because root surface ecology is generally accepted as a subject of great potential promise (Bowen and Rovira 1976; Tinker 1980a, b), but it will not fulfil this so long as it remains a collection of isolated and partial observations. The finding that *Azotobacter* species are more numerous on mycorrhizal than non-mycorrhizal roots (e.g., Bagyaraj and Menge 1978) and that there are consequential improvements in host growth, are especially interesting and need further investigation.

The most important practical aspect of biological interactions is probably the relationship with pathogens (Schonbeck 1979). Simple mechanical protection of the root surface can be postulated for ECM, but there are a number of other hypotheses, including, of course, improved plant nutrition (see Mosse *et al.* 1981). Broadly, mycorrhizas appear to provide some protection against fungal and bacterial root pathogens and nematodes, but make infected plants more easily attacked by leaf pathogens and viruses. Once again, the confused state of the topic demands careful investigation of infection processes over a range of conditions, rather than simply comparing degree of attack with and without mycorrhizas.

Techniques

No major new advances appear to have been made, but it is worth noting that Giovanetti and Mosse (1980) have compared different published methods of estimating percent infection with VAM in root systems, and, as expected, have concluded that a variant of the line intersection method is the best. The counting of entry points appears to be becoming more popular as a method of defining infection levels.

Host-Fungus Interaction

Uptake, Translocation and Transfer of Nutrients

The basic processes involved in altering the host growth and yield are now well established, and no major changes have taken place recently. These are in the great majority of cases due to an increased supply of phosphorus to the host, and yield improvements are normally only obtained when the host is phosphorus-deficient (see Tinker 1980a, b). There is also evidence that zinc (Tinker 1978; Rhodes and Gerdemann 1980) and now copper (Timmer and Leyden 1980; Gildon and Tinker, in preparation) can be supplied to the host, and that this can increase its growth if these elements are deficient.

The main process of nutrient supply is now well understood. The external hyphae absorb nutrient from the soil, translocate it to the internal fungal structures, and from there it is transferred to the host. The uptake processes have scarcely been examined as yet, but there is some evidence that the uptake kinetics of the fungal tissue for phosphate may differ from that of uninfected root, with a much smaller value of the constant K_m (Cress *et al.* 1979) where the

$$\text{Uptake rate } S = \frac{S_{max}\ C_l}{C_l + K_m}$$

and C_l is the external solution concentration. There may be various alternative explanations for their results, such as the existence of a very strong local sink for phosphorus in the fungal structures in the root, but it seems quite possible that the effect is real. It has also been suggested that mycorrhizal root can absorb phosphate from soils so deficient that none is taken up by non-mycorrhizal roots (Mosse 1973). If so, this would give a further reason for the efficiency of phosphate uptake by mycorrhizal roots from very deficient soils, though the major effect is undoubtedly the greater amount and better distribution of absorbing surface and the consequent by-passing of the diffusive impedance for immobile ions in the soil. This view avoids any assumption that the mycorrhizae can "solubilize" or render more "available" any soil nutrient, which accords with an increasing number of experiments which show that the L value for infected and uninfected plants was the same (see Tinker 1978). This view is supported by Barrow *et al.* (1977), who found that infected and uninfected plants were equally able to use phosphate which had been strongly sorbed on the soil. Surprisingly, no parallel work appears to have been done for the ectomycorrhizas yet.

These ideas have been supported by much work on translocation in the hyphae (Tinker 1975; Rhodes and Gerdemann 1980). Earlier studies by Melin and co-workers (see Harley 1969) established that phosphorus, calcium and nitrogen were translocated in the mycelium of ectomycorrhizas, and the movement of zinc in rhizomorphs of ectomycorrhizas has been shown (Bowen *et al.* 1974). Direct measurements have determined fluxes of phosphorus, sulphur and zinc in VAM hyphae (Cooper and Tinker 1978) and the movement of calcium in VAM hyphae is inferred (Rhodes and Gerdemann 1978a).

The potential benefit to the plant then depends both upon whether the fungus can absorb, translocate and transfer the element of appropriate rates, and also upon whether the element can equally well be transported to and aborbed by the simple root. The latter is usually true for elements which are mobile in soil, and Rhodes and Gerdemann (1978b) showed that though sulphur was absorbed rapidly by VA mycorrhizas, this was of no particular advantage to the host, which was well able to absorb sufficient through its uninfected roots. The general hypothesis was stated by Sanders and Tinker (1973); a mycorrhizal response can be expected when the mean inflow (uptake rate per unit length of root) required for a plant to grow at its maximum rate was greater than could be supplied by the soil by diffusion and mass flow, and this still appears to be acceptable. Yost and Fox (1979) in a very valuable piece of work examined the soil solution concentration at which various field-grown crops first started to benefit from mycorrhizal association. These ranged from 0.1 μg P/ml for soyabean to 1.6 μg P/ml for cassava and *Stylosanthes*. The last value suggests an unusually large required mean inflow for these crops, but without detailed plant and soil data no accurate calculations can be made. The values are generally of the order of magnitude expected on the above hypothesis. The possibility has also been raised that soil analysis results used for predicting phosphorus dressings for mycotrophic crops should be adjusted to take account of the expected level of VAM infection, because correlations between growth and bicarbonate-soluble P in the soil were much improved when VAM infection in leeks was controlled (Stribley *et al.* 1980).

Despite the range of elements mentioned above, phosphorus occupies a special position. In part this is because it is the most immobile major nutrient in soil, but it is also likely that phosphorus has a special transport system in the hyphae, due to the formation of polyphosphate in the vacuoles (Tinker 1975a). Polyphosphate accumulation also occurs in the ECM (Chilvers and Harley 1980).

Effect on Water Use

There have been a number of suggestions that mycorrhizas enhance water uptake by roots from dry soil and thereby minimize the effects of drought (Reid 1979). Some fungi are undoubtedly more drought-resistant than higher plants (Uhlig 1972) and could possibly absorb water and transfer it to the host. The mathematics of water transport to roots in soil is closely analogous to that for phosphate diffusion, so that a similar theory could be elaborated for water. Reid argues that mycorrhizal hyphae could carry water into the root, and bridge any gaps that form between soil and root (see Tinker 1980a for discussion), as root hairs do. However, whereas there can be hundreds of root hairs per cm of root, there may only be of the order of 10 VAM entry points per cm. Cooper and Tinker (1981) found that transpiration by the host increased P flux in the external hyphae, which implies there may be a bulk flow of hyphal contents towards the root. However, even if this is true, they estimated the flow rate was only of the order of 10^{-6} ml/day for 2 hyphae, which is probably well below the rate necessary to constitute useful amounts of water for rapidly transpiring plants. As so often, it is not a question of whether an effect happens, but whether it is important, and it seems that water uptake by VAM hyphae could possibly be useful for the survival of natural vegetation, but is unlikely to contribute to the growth of agricultural crops. There is a well-established connection between drought tolerance in plants and their phosphorus status (Atkinson and Davidson 1973), which probably explains many of the reported effects. Levy and Krikun (1980) found that the stomatal conductance of plants recovering from water stress was larger when they were infected with VAM, and ascribed this to effects on the hormonal balance. The infected and uninfected plants were stated to be of the same size, but unfortunately no data on mineral composition were given.

Use of Host Photosynthate

Observations on root surface ecology immediately raise the question of whether the presence of mycorrhizal fungi increases the quantity of root "exudates" (Rovira *et al.* 1979) which support the non-symbiotic inhabitants of the rhizosphere. Bacterial infection of sterile roots is known to cause increased losses of carbon into the rhizosphere. There is much work which suggests that very much larger amounts of plant carbon are directed to the root systems with ECM than without (Harley 1975; Fogel 1979), but at present there does not appear to be any direct measurements of the amounts lost as exudates, in addition to that respired or used in fungal biomass. Equivalent measurements of such losses with VAM are more difficult to make, but the distribution of carbon in mycorrhizal and non-mycorrhizal plants has been compared (Pang and Paul 1980; Snellgrove, Splittstoesser, Stribley and Tinker, in preparation) and it seems likely that extra amounts, of the order of 10% of total carbon fixation, are diverted to the roots when they are infected, and that perhaps 1 or 2% of the fixed C can be detected in the soil 48 hr after feeding $^{14}CO_2$. After longer periods, the amount in the soil is less, and more can be collected as CO_2, as would be expected. The only evidence against this suggestion of a more active exudation in mycorrhizal plants is that Ratnayake *et al.* (1978) found that plants with a high percentage phosphorus in their tissues release less organic compounds than if they had a low phosphorus percentage. It is usual for VA mycorrhizal plants to have a larger phosphorus percentage even than phosphorus-fertilized plants of the same size and, of course, much larger than non-fertilized non-mycorrhizal plants on the same soil, so this would suggest greater leakage by non-mycorrhizal plants. No firm conclusion about exudates can be reached until direct measurements are made, but it is quite certain that considerable amounts of photo-synthate may be used by the mycorrhizal fungus, especially by ECM.

Effects on Host Growth

The general outlines of the supply of phosphorus to the host by VAM are well documented and reviewed, and have in part been dealt with above, but a few special aspects will be discussed. Baylis (1975) suggested that nutritional dependence upon mycorrhizal infection is connected with root branching and root hair proliferation and this has recently been supported by St. John (1980). Those species with poorly branched roots with few or no hairs (magnolioid) will necessitate a large inflow to maintain the plant and will consequently require mycorrhizas to supply it, in agreement with the hypothesis already outlined. Crops which give yield responses to infection are frequently of this type (e.g., *Allium*), and tree species with ECM in general have very low root densities (Nye and Tinker 1977). Conversely, plants with finely divided external roots, especially if they have many root hairs, should be quite able to absorb phosphate at a sufficient rate for growth, and would not need mycorrhizas. The largest group of plants with such root systems are the *Gramineae*, and it is indeed found that large and repeatable growth responses in this group are relatively rare. This theory implies that non-responsive species should respond little or not at all to phosphate fertilizer also. However, in recent work in pots and in the field, we have found that wheat gives only very small responses to VA infection in sterilized soil in the field, even under conditions when P fertilizer gave a 200% growth response. The final infection in the wheat roots was up to 50% so a response was not prevented by low infection. Mosse *et al.* (1981) also noted that some *Gramineae* (e.g., *Paspalum* and maize) have extensive root systems, with ample root hairs, but nevertheless respond readily and strongly to mycorrhizal infection. This point requires to be fully established because if correct, we must start to consider a possible inherent lack of efficiency in the symbiosis in at least some crops, and the above hypothesis may no longer be applicable in all cases. The efficiency of the response mechanisms thus needs more investigation, along the lines used by Sanders *et al.* (1977), in which an attempt was made to analyze the efficiency of different endophytes in terms of phosphorus inflow, mycelium quantity and infection spread. Similar concepts should now be applied to comparisons between hosts. The differences between isolates or strains of the fungi are paralleled by important differences between responses of host plants of different cultivars (Bertheau *et al.* 1980), and the mechanisms here also need investigation. It is certainly worthy of note that two crops formerly believed to be particularly able to grow on infertile soils, cassava and *Stylosanthes*, have been shown to be almost wholly dependent upon VAM infection for normal growth (Yost and Fox 1979; Van der Zaag *et al.* 1979; Howeler *et al.* 1979). This must have enormous implications for the practical application of knowledge of mycorrhizas. Important responses seem to be found especially frequently with legumes, where there are clear effects on the rate of nitrogen fixation (Smith *et al.* 1979, and reference given by them). There may be some special relationship between formation of mycorrhizas and leguminous nodules, since Schenk and Hinson (1973) found that only nodulating lines of soyabean responded to VAM inoculation. There has been a report that N-fixing ability has been obtained in *Rhizopogon* mycorrhizal with *Pinus radiata* (Giles and Whitehead 1977), but this potentially very important claim awaits confirmation. The question of the mechanisms by which the internal concentration of nutrients in plants is controlled has not been settled, though there is growing interest in it (Nye and Tinker 1977, p. 126 and 215). It is accepted that mycorrhizal infections usually increase the plant phosphorus concentration at the same time that they increase plant growth. However, Stribley *et al.* (1980) pointed out that there are many pot experiments which show that the phosphorus concentration in mycorrhizal plants is increased above that in plants given fertilizer phosphorus such that they grow to the same size as the infected plants. If it is confirmed for field grown crops, it has very interesting implications for the value of plants as human and animal food, and for the assessment of the efficiency of a given amount of phosphorus in the production of plant dry matter. The reason is as yet uncertain, but Stribley *et al.* (1980) suggested that it could perhaps arise if the fungus required some of the host's photosynthate, and thereby necessitated a higher phosphate percentage to maintain the photosynthetic rate necessary to provide it. This effect would then depend upon whether the host could compensate for the added photosynthate drain or not, and could perhaps explain some of the complicated and variable results relating to changes in growth and phosphorus concentration. Pairunan *et al.* (1980) found this effect with superphosphate, but not with rock phosphate, so the solubility or timing of the phosphorus supply may be involved also.

There has always been a strong interest in the ability of mycorrhizal plants to use poorly soluble forms of phosphorus. This was a very popular topic at one time (Hayman 1978; Tinker 1980b) but rather less work has emerged on it recently. The studies with the most extensive comparisons are probably those of Sparling and Tinker (1978c) and Pairunan *et al.* (1980) with clover. In both cases the comparative pattern of responses by infected and non-infected plants to superphosphate and rock phosphate was similar. In Sparling and Tinker's results, the percentage increase in yield from inoculation declined rapidly as either form of phosphorus was added, and the final yield with 2.3 g P/kg soil as rock phosphate was only a little less than that with 0.5 g P/kg soil as superphosphate. The results of Pairunan *et al.* (1980) showed at first a surprising increase in the percentage response to inoculation with either form of added P, but again this declined later, and the final yields with 0.8 g P/kg soil as superphosphate or 29 g P/kg soil as rock phosphate was not greatly different. In general, this agrees with the argument of Tinker (1975b), that if mycorrhizal hyphae simply permeate the soil more densely than roots, then their advantage is that they lessen the mean distance between any rock phosphate particle and the nearest absorbing surface. If so, very fine subdivision of the rock phosphate, or the addition of very heavy rates, should be able to supply P at the same rate to infected or uninfected plants. At intermediate rates infected plants respond much better than uninfected. It follows that mycorrhizal plants would not use phosphorus sources so insoluble that they were of no value to the non-mycorrhizal plant, but that they could well use sources of moderate solubility more efficiently. However, we still await careful physicochemical studies on this point and until these are done, our information is partial, empirical and not easily applied.

The question of trace elements supply is still important; indeed, the supply of zinc to citrus seedlings in fumigated nurseries is one of the very few cases in which real commercial advantages have been shown by mycorrhizal inoculation. It is known now that copper also can be supplied to hosts by

VAM, but most trace element deficiencies are rather easily corrected with small additions of the element, so this is unlikely to be a very important practical application. The well-known nutritional interactions of copper and zinc with phosphorus have also been studied, and shown to be in part caused by the effect of phosphorus on VAM and hence on trace metal uptake (Lambert *et al.* 1979; Timmer and Leyden 1980).

There is still much interest in the possibility that mycorrhizas have effects on their hosts which are not mediated by any of the processes dealt with above (e.g., see Hayman 1980). Such effects need to be shown convincingly in experiments where all nutritional effects are fully allowed for. The suggestion is that chemicals with phytohormonal properties are produced by mycorrhizas; this is certainly true for the ECM (Slankis 1973), and Allen *et al.* (1980) have found that there are larger concentrations of hormones present in plants with VAM. However, these suggestions have been made for a number of years now, and it begins to be rather surprising that they have not been conclusively proven yet, if they are indeed of great importance, though Hayman (private communication) has recently found responses to inoculation in peas which could not be fully reproduced by any dressing of phosphorus.

Competition between Host Plants

The mechanics of competition between plants for light, nutrients and water are well established, though the analysis of any particular situation is often difficult. It is obvious that the existence of a symbiosis of different relative value to two hosts will alter their competitive ranking, and that a general symbiont such as VAM could affect the whole species balance of a community when the availability of phosphorus is growth limiting. The different value of mycorrhiza formation to different hosts in the same soil is now well established, e.g., clover always benefits more than grasses (Crush 1974; Sparling and Tinker 1978b, c; Powell 1979). Fitter (1977) tested this directly by growing *Lolium perenne* and *Holcus lanatus* together in sterile soil and showing that the latter was greatly advantaged relative to *Lolium* when VAM inoculum was introduced. The position is however very complex, in that the level of infection of a host may depend upon the presence of other higher plants (Christie *et al.* 1978). The analysis of the natural situation, in which a range of hosts compete in the presence of the inoculum of a range of mycorrhizal fungi, has not been attempted. This complexity is emphasized even more with perennials carrying ectomycorrhizas, in which a succession of different fungi may become dominant at different times in the growth of the host (Foster and Marks 1967).

Practical Applications

As a research topic, VAM is urgently in need of some major and obvious practical applications. Significant responses to infection with VAM have been obtained on many crops, including wheat, barley, maize, soyabean, rice, cotton, tomato, potato, onion, groundnuts, cowpea, beans, white clover, alfalfa, stylosanthes, *Centrosema*, *Pueraria*, ash, cherry, *Liriodendron*, maple, *Coprosma*, apple, citrus, peach and grapewine. The great majority of this work has been in pots, and the critical question is why this has not been balanced by similar reports of responses in the field (Rhodes 1980). The most obvious reason is that efficient native endophytes are present in the soil in sufficient numbers, but the fairly frequent responses obtained in pots even with unsterilized soils e.g., Mosse *et al.* 1969; Powell 1977) make this a little unlikely to be the sole explanation. It is conceivable that the handling or storage of such soils may diminish the natural inoculum concentration, so that these pot-grown plants are less fully infected than ones grown in the same fresh field soil. Temperatures and water relations may be different in the greenhouse than in the field, and may encourage infection levels in inoculated plants above what could be obtained under field conditions. Finally, it is a common occurrence that responses to fertilizer treatment in pots cannot be duplicated in the field, and this is normally explained by the additional stress caused by the rapid uptake rates needed for a vigorously growing plant occurring in a very limited volume of soil. For these reasons, pot experimentation, especially on sterilized soil, is no real guide to the behaviour of inoculated plants in the field, except that if such responses cannot be obtained in pots, they are exceedingly unlikely to be found in the field.

Recently Lambert *et al.* (1980) tested and introduced endophytes into three soils, and found that in general the indigenous fungi were best at promoting host growth, and that differences between the fungal populations diminished with time, suggesting that some claimed improvements of growth by inoculations with different fungi may not have been examined extensively enough.

Some progress has been made. In New Zealand, Powell and Daniel (1978) tested field inoculation of clover, and found good responses. Hayman and Mosse (1979) have also tested inoculation of clover in upland pasture in Britain, and similarly found good responses, though some sites gave no response. Permanent grassland could be an important application of VAM inoculation, because of the low soil phosphate, and the small value of the crop per hectare, which may make phosphate fertilizing uneconomic. There are some hopeful results now for field crops also. Most of these are on soils either very low in phosphorus, and/or on soils with very low natural levels of VAM infection, so that they may not have much relevance to practical agriculture, but some responses are in more normal circumstances (Owusu-Bennoah and Mosse 1979). These workers found responses in three crops, including up to 6-fold increases in growth of lucerne inoculated with *Glomus caledonius*. Nevertheless, none of these workers, up to the present, have considered that their results have proved that an economically important effect could be obtained in practical agriculture. This situation is in sharp contrast to that relating to the ECM, where the advantages of seedling inoculation are well authenticated, and where pure inocula of single species can give useful responses in the field (e.g., Marx *et al.* 1978). This may simply reflect the shorter history of such research with VAM than with ECM, but the difference is more probably due to the ubiquity, the non-specificity and the persistence of the VAM propagules, which occur in all soils which have not been artificially altered. This last point has caused a spate of interest in VAM for the revegetation of mine spoil heaps, gravel pits and other disturbed environments. Further, it has given grounds for optimism over the value of inoculation with VAM where the soil situation has been sharply altered by normal agronomic practices, e.g., change of pH, drainage, or the prolonged growth of non-host crops.

The use of mycorrhizas on artificially sterilized soils is clearly very promising, but the actual scale of the application is rather small. In most nurseries which are fumigated, natural re-infection will take place, though artificial infection may be worth while for the first crop. If general fumigation processes become more popular against disease, the scope for use could increase. The early infection of seedlings of many species which are pot-grown in sterile media would seem to offer possibilities of better establishment in the field; however, if these media are well fertilized, the plants may gain no benefit from the inoculation whilst in the pot, and it may even be difficult to get infection established (Rhodes 1980).

Two matters which presuppose the existence of suitable markets for VAM inoculum are already receiving attention. These are techniques for growing pure inoculum, and estimates of the rate of spread of infection are established. Inoculum may be produced by an enlargement of the normal 'stockpot', by growing inoculated plants in large containers of sterile sand or soil (Sanders, private communication). A more radical departure is the growing of infected plants in flowing solution culture (Elmes and Mosse 1980) to yield large amounts of clean infected roots. It seems unlikely that mycorrhizal inoculum will ever be as easily handled as Rhizobium inoculum, because of its heterogeneity, and the large size of spores, but growth of the VAM fungi in pure culture might produce a more easily handleable material. So far attempts have been made to mix inoculum with moduled balls of soil (Hall 1978; Powell 1979), or to stick it onto seeds (of citrus) with a cellulose adhesive (Hattingh and Gerdemann 1976).

This problem with inoculum means that only relatively small numbers of propagules can possibly be provided for any large-scale inoculations, for example, on extensive hill pasture. The rate of spread of the infection can be of great importance in these circumstances. The first measurements were reported by Sparling (1976), who found that infection by *Glomus mosseae* moved down through a mixed grass-clover sward at a rate of about 1 cm/week when grown in greenhouse conditions. More recent measurements by Powell (1979) and by Warner (1980) agree with this order of magnitude, but Powell's results indicate that the prior presence of another mycorrhizal fungus will greatly reduce the rate of spread. At this rate, sparsely spread inoculum may only infect a fraction of the total vegetation in the first year at least, unless other mechanisms of spread operate, such as movement by soil fauna.

Conclusion

Two points seem to arise from this review, which suggests that the current large investment in mycorrhizal research may not be giving quite as much progress as we should expect. Firstly, basic research must be aimed at defining much more extensive principles and generalizations rather than obtaining disconnected items of information. Further reports of isolated pot trials are of little general value, though they may be important for particular hosts and conditions. Secondly, applied research should be prosecuted with a singleminded vigour in an attempt to discover more economically useful applications. This need for a number, however small, of tested applications of economic value arises because the upsurge in mycorrhizal (especially VAM) studies has undoubtedly been justified in many instances by suggestions that great practical benefits are obtainable. If such hopes are too long deferred, there could be a reaction amongst research managers against such work. A balanced position seems highly desirable (Hayman 1980) because it may indeed be found that most of the potential benefits of mycorrhizas are already being obtained naturally in the majority of conditions.

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