Influence of Soils and Fertility on Activity and Survival of Vesicular-Arbuscular Mycorrhizal Fungi

D. S. Hayman

Soil Microbiology Department, Rothamsted Experimental Station, Harpenden, Hertfordshire, AL5 2JQ, England.

The group of fungi that form vesicular-arbuscular (VA) mycorrhizae are among the most common soil fungi and probably infect more plant tissue than any other fungal group (12). Increased recognition of this situation has attracted many plant pathologists to work on VA mycorrhiza, along with other plant scientists interested particularly in the frequently beneficial interaction between VA mycorrhizal fungi and their plant hosts. The advance of these fungi from their first appearance in the fossil record to present-day occupation of most geographical regions, habitats, and plant species is evidence of phenomenally successful activity and survival. These aspects will be examined in this review with emphasis on the ways that soils and soil fertility influence the ecology and symbiotic behavior of VA mycorrhizal fungi.

OCCURRENCE IN DIFFERENT SOILS

The extensive activity and survival potential of VA mycorrhizal fungi in most naturally occurring plant populations on undisturbed soil is immediately obvious from an examination of the roots of the vegetation present (27). They can infect most species of flowering plants in most habitats. Thus, VA mycorrhizal fungi are generally abundant in grasslands, savannas, scrub and open woodlands, dense rain forests, semideserts, and sand dunes. By contrast, they are rare in north-temperate podzols that support almost pure stands of ectomycorrhizal trees, in acid heathlands dominated by plants with ericoid mycorrhiza, and in very wet soils. Their populations vary in disturbed soils such as coal mine spoils and old road beds. They often produce large resting spores whose numbers range widely; eg, from six to 1,590 spores (>100 μm diameter) per 100 g of soil in New Zealand grassland, scrub land, and forest soils (17). As VA mycorrhizal fungi are found in almost every soil type, it is not surprising that on a global scale they are virtually ubiquitous. They are found in tropical, temperate, and arctic soils, and even individual species can have a world-wide distribution.

In cultivated soils, VA mycorrhizal fungi are affected by various agricultural and horticultural practices, particularly fertilizer additions, pesticide applications, and crop rotations. Changes in soil fertility due to amendments with mineral fertilizers or organic matter can markedly affect the activity of the soil mycorrhizal population in terms of the amount of root infection and numbers of resting spores produced. There is some evidence that organic matter added to soil leads to better mycorrhizal development. Conversely there is considerable information on the negative effects of nitrogen fertilizer on mycorrhiza formation. For example, in the heavy clay loam soil on the Rothamsted Farm (Little Knott field), monthly samples from wheat plots showed nitrogen (as ammonium nitrate) markedly decreased both VA mycorrhizal infection and spore numbers (15). In these plots, mycorrhizal infection built up slowly in the spring and reached a plateau in the autumn, whereas numbers of spores increased dramatically in midsummer. Probably spore production increases as root growth slows down or partly ceases. The adjacent Broadbalk wheatfield at Rothamsted also showed the negative effect of nitrogen fertilizer on the indigenous mycorrhizal population (15). In addition, there was a marked negative effect of nitrogen on the mycorrhizal spore population in a wheat field in the light sandy soil on the Woburn farm near Rothamsted (Stackyard field), but there was no effect of N in another Woburn field (Butt

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0031-949X/82/08111907/$03.00/0

Furlong) planted with field beans (*Vicia faba*), a crop that fixes its own nitrogen (16). More recently, samples collected from barley growing in Butt Furlong showed a strong negative effect of N on mycorrhiza which overrode effects of other soil amendments such as aldicarb which is a nematicide/biocide.

Kruckelmann (24) obtained contrary effects in two soils he examined. His samples from Broadbalk (Rothamsted Farm) showed the same negative effect of N as reported previously (15) and also a negative effect of farmyard manure (FYM) calculated to be equivalent to 224 kg N/ha. By contrast, in a soil at Braunschweig (Germany), he observed an increase in spore numbers in the presence of mineral fertilizer (providing 40 kg N/ha), FYM, or composted municipal refuse. These opposite effects in different soils are probably due to differences in the basic fertility of the soil. To predict the effects of adding fertilizer on the population of mycorrhizal fungi, some idea of the initial soil fertility is needed because, in a very poor soil, spore production will be limited by the small amount of total, not the percent, root infection resulting from poor plant growth.

Bevege (4) showed that the nitrogen picture can become more complicated when interactions with phosphate are taken into account. In field plots of *Araucaria cunninghamii* (hoop pine) in northeastern Australia, he found a trend of increased VA mycorrhizal infection with increasing additions of N (448 to 4,032 kg N/ha as urea) at intermediate levels of P (37 and 74 kg P/ha as superphosphate), but at 148 kg P/ha infection decreased with increasing N. The largest numbers of spores were formed at high and low levels of N. The generally inhibitory effect of N on infection by mycorrhizal fungi contrasts with its tendency to increase infection by root pathogenic fungi; eg, *Fusarium solani* f. sp. *phaseoli* (44).

Field studies at Rothamsted on the effects of phosphate fertilizers on the indigenous mycorrhizal populations have also shown negative effects (16), but they were less consistent than with N. Data from the Broadbalk field suggested this with 5–10% mycorrhizal infection in the N + P plots compared to 13% with N alone, but more details were obtained for Great Field IV at Rothamsted (16). Here there were two trends: viz, most mycorrhizal infection in plots given the least P, and the largest number of spores in plots given intermediate amounts of P. Roots of swede (rutabaga) had no infection, although numbers of spores did not drop greatly in the swede plots.

Less consistent effects of P compared to N fertilizer were also shown by Bevege (4) who found fewer VA mycorrhizal spores in soil given no P than in soil amended with various levels of superphosphate. Kruckelmann (24) found that applying amounts of phosphate ranging from 0 to 220 kg P/ha for seven consecutive years did not affect the frequency of VA mycorrhizal spores in soil where rye was grown 11 yr later, although there was a trend towards a reduction at higher levels of P in the soil. Sparling and Tinker (39) observed no effect of N fertilizer, but a negative effect of P (triple superphosphate or basic slag) on VA mycorrhiza in hill grasslands in England. The negative effects of P on VA mycorrhizal fungi in soil appear more pronounced in experiments with potted plants in which the phosphate probably inhibits the fungus by raising P levels in the plant more than in the soil.

Strzemska (41) made detailed studies of cereals and legumes for several years in agricultural soils in Poland and found a consistent negative effect of NPK fertilizer on the intensity of mycorrhizal infection within the roots of four cereals, but not beans. This supports the results obtained with nitrogen in Woburn soils.

Although quite specific effects of soil fertility have been clearly demonstrated many times at specific sites, it is difficult to find consistent relationships between VA mycorrhiza and soil fertility at separate sites. Generally, high soil fertility leads to little VA mycorrhizal infection so that we are unlikely to find much mycorrhiza in intensively cultivated soils. However, some crops are heavily mycorrhizal, even in very fertile soils; eg, maize in the midwestern USA. Observations at several sites in southern Spain (18) showed no relationship between levels of mycorrhiza formation and soil fertility except for adjacent plots within an individual site. Thus, VA mycorrhiza was often abundant in both poor and rich soils, which shows that low soil fertility is not always a prerequisite for extensive mycorrhizal development.

SURVIVAL

VA mycorrhizal fungi have not yet been cultured axenically and are generally considered to be obligate symbionts in plants. Nevertheless, their sheer abundance is indicative of an impressive capacity for survival in spite of their dependence on higher plants.

What then are the forms of propagule that can survive and retain infectivity? The large resting spores, which form the basis for the taxonomy of the V mycorrhizal fungi (cf. J. Trappe [45]), are the most obvious forms. Others include infected root fragments, infections in living roots, and clumps of hyphae. Mycelium and infected roots are obviously important in the survival and activity of nonsporulating endophytes, but they may also represent a considerable proportion of the inoculum potential of the spore formers. Thus, there is sometimes a correlation between numbers of spores and mycorrhizal infection or soil infectivity (15), and sometimes not (21). Hence a wide range of techniques are needed to give a full picture of the activities of VA mycorrhizal fungi in soil. Methods include root examination after differential staining, recovery of spores by wet-sieving or other procedures, and baiting with appropriate host plants. Porter (30) adopted the most probable number technique to estimate the population of infective propagules and found that this coincided with spore numbers in one soil, but not in another.

The large thick-walled resting spores probably survive in soil for long periods, even in extreme environments. Some species are active at low field soil temperatures and build up during the winter around the roots of perennial host plants such as lucerne and red clover (D. S. Hayman and C. A. Clarke, *unpublished*). The absence of a large decrease in spore numbers in soil cropped with the nonhost swede (16) suggests that they can survive at least 1 yr in the field, although populations fell during 2 yr with a nonhost or during a fallow (5). In cultures maintained on stock plants in the glasshouse, numbers of spores usually peak within 1 yr of inoculation and drop substantially thereafter. Hyperparasites may decrease mycorrhizal spore numbers in some situations. Ross (36) found that adding 5% unsterile soil to previously inoculated steamed soil reduced sporulation of *Glomus* sixfold and that of *Gigaspora* by 93%. Separation of the VA mycorrhizal fungi from unsterile soil by a membrane with 0.2 μm diameter pores nullified this effect, indicating that the factor suppressing sporulation was not diffusible. Although soils suppressive to certain pathogens (eg, *Gaeumannomyces graminis* and *F. solani*) are well known, this phenomenon is less well known for mycorrhizal fungi, and knowledge of that kind may help to interpret some of their irregular distribution patterns in soil.

Spores of different species or strains of VA mycorrhizal fungi differ in ability to germinate on agar, for example, which is partly affected by external nutrients and unknown dialyzable factors from soil, and is often optimal at soil temperatures near those of the location where they were isolated. Some spores can produce several germ tubes simultaneously, thereby increasing the chances of the fungus encountering a root and maintaining or expanding its activity, whereas others can produce successive germ tubes over a period of time if the first ones fail to find or infect a suitable root. VA mycorrhizal resting spores are the largest fungal spores known; they are full of nutrient reserves and their individual survival potential is high, which perhaps compensates for the relatively small numbers produced compared to many other fungi.

Infected root fragments have been used as inocula in many experiments with VA mycorrhizae. Infection of seedlings from freshly cut pieces of mycorrhizal root is often more rapid than from resting spores (14). The longevity of VA mycorrhizal root pieces and their regeneration potential is often debated. Recently Tommerup and Abbott (43) showed that 1- to 6-mm pieces of subterranean clover root infected with *Glomus fasciculatus*, *G. monosporus*, or *Gigaspora calospora* remained infective after 6 mo of storage in dry soil; new hyphae emerged from inside the old

hyphal tubes. Similarly treated roots infected with *Glomus caledonius* or *Acaulospora laevis* did not remain infective, however. A substantial loss of viability of mycorrhizal root fragments occurred after 3 yr in topsoil stored during opencut mining, propagule numbers being 8–10 times greater in the undisturbed soil (35). It appears that a major means of spread of mycorrhizae in this soil was between infected root fragments and roots of uninfected plants because the actual spores (*G. fasciculatus*) were much less affected by storage.

VA mycorrhizal hyphae form an extensive network in soil. In the rhizospheres of ryegrass roots, Tisdall and Oades (42) measured about 55 m of these hyphae per cubic centimeter of soil. Read et al (34) believe that it is the root-based hyphal network in soil, rather than resting spores, that is responsible for infecting seedlings that become established in a natural grassland sward. Earlier work by Clark (7), in which passing forest soil through a 9.5 mm sieve drastically reduced its infectivity towards *Liriodendron tulipifera*, suggested that most indigenous infection came from the hyphal network because the hyphae, but not the spores or infected root pieces, would have been appreciably damaged by sieving.

There are two recent reports which suggest that the hyphae of VA mycorrhizal fungi may have the ability, albeit limited, to grow in soil independent of a plant root. Warner and Mosse (47) showed infection of clover seedlings from hyphae detached from bags of inoculum from which the hyphae had grown about 1 cm into the soil. Ocampo and Hayman (29) found that inoculum kept 10 wk in the glasshouse in soil with no plants or with the roots of nonhost plants was more infective than the same inoculum stored at 2 C, a routine storage method not previously found to reduce inoculum viability. Possibly the soil organic matter may be a major maintenance substrate that enables VA mycorrhizal fungi to remain active and ready to infect a susceptible root. In this respect, minimum tillage and direct drilling techniques, which disrupt the mycelial network far less than plowing, might favor the survival of a native mycorrhizal population already selected and expanded on a strongly mycorrhizal preceding crop.

Effects of the soil fauna on VA mycorrhizal activity should not be ignored; some collembola and possibly nematodes can feed upon some of the soil-based mycelium attached to the root and so reduce mycorrhizal activity. This may partly account for some reports of nematicides increasing mycorrhizal populations in arable soils.

The distance that VA mycorrhizal fungi can spread through soil is of the order of 0.6 to 3.2 m/yr (33). In the glasshouse, Warner (46) found that increasing root density generally favored spread except at very high densities. Soil moisture and texture had less effect than host species on spread. The maximum interroot distance over which hyphae could extend from an infected plant to an indicator plant was between 2 and 3 cm.

Difficulties in predicting levels of indigenous VA mycorrhizal populations in different soils arise from the large number of factors that can effect their distribution, activity, and survival. These include soil fertility; soil moisture; pH; plant susceptibility; light intensity; altitude; soil organic matter, depth, and disturbance; physical movement by water, earthworms, and the soil microfauna; and random variation. Random variation makes it necessary in quantitative studies to bulk many subsamples of soil.

ENDOPHYTE ADAPTABILITY

The wide range of VA mycorrhizal fungi in many natural habitats suggests a degree of ecological equivalence between species (17,25). Likewise, similar agricultural soils growing the same crop may contain different species, even in adjacent fields (eg, Broadbalk and Little Knott fields at Rothamsted). Nevertheless, certain soil factors can favor specific endophytes. For example, the distribution of "honey-colored sessile" and "yellow vacuolate" spore types in Western Australia was related to soil pH (1). Farmyard manure favored the "yellow vacuolate" spore type in Broadbalk field at Rothamsted. Furthermore, chemicals added to agricultural soils can change the species composition as well as the total size of the mycorrhizal population, and the indigenous mycorrhizal populations of natural soils are often very sensitive to soil amendments.

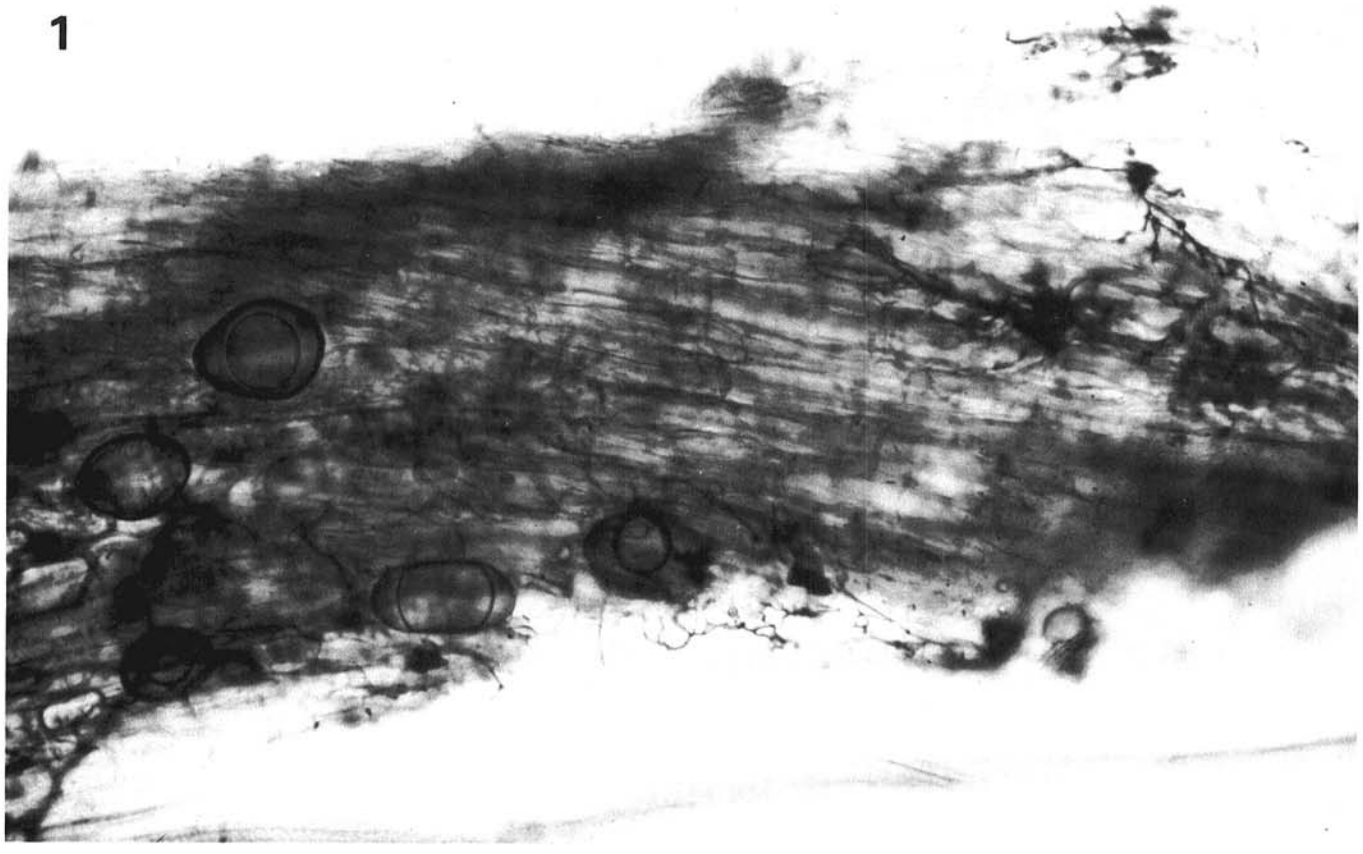
Of the four endophytes in Broadbalk soil, the white reticulate one is far more sensitive to added fertilizer than the other three. This recalls the extreme sensitivity to N of the native mycorrhizal population of the Woburn Stackyard wheat plots, where the white reticulate endophyte predominated. Different endophyte species also vary in infectivity in soil treated with different fungicides (40). These and other studies suggest the possibility of manipulating soil populations of VA mycorrhizal fungi both qualitatively and quantitatively. If a crop is benefitting from the native mycorrhizal infections, some chemical amendments could be counterproductive. On the other hand, if the native endophytes are not symbiotically efficient, but compete well with the introduced endophytes, a chemical agent could be useful to suppress the native ones before inoculating field crops with the more favorable introduced endophytes. It is important, but difficult, to monitor the fate of inoculant fungi in soil. Some can be differentiated anatomically and others may be distinguished by immunofluorescence techniques currently being developed. Mixed infections are not uncommon; distinctly different endophytes can readily occupy the same root and even the same small area of root cortex (Figs. 1 and 2). In other mixed infections, one endophyte may inhibit another, but little is known about such interactions.

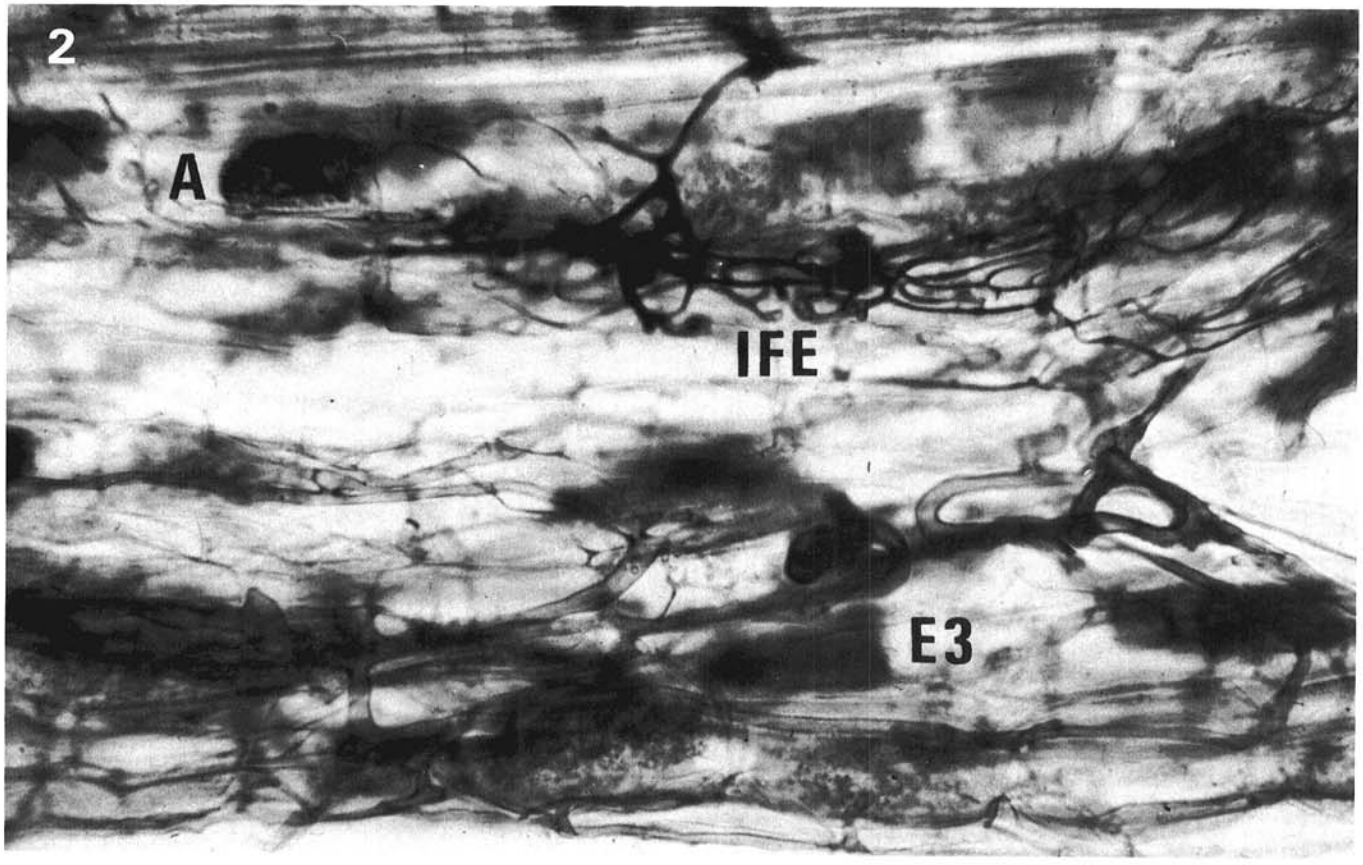
In poor, marginal soils where both plants and endophytes have adapted to nutrient stress conditions, the VA mycorrhizal fungi may show poor tolerance to added nutrients and increased soil fertility. An example of this was discovered in the hill pastures of mid-Wales where Hayman and Mosse (20) observed more mycorrhizal infection in the natural rough grassland than in amended areas that had received lime and fertilizers. However, the root infection in the amended soil differed anatomically from that in the untreated soil, suggesting a selection by the plants of different endophyte species better adapted to more fertile soil. Strains of *Glomus mosseae* and *G. fasciculatus* introduced as inoculum at these sites were less sensitive to soil applications of lime and phosphate than were the indigenous endophytes.

Long-term application of superphosphate fertilizer (15 yr of 150 kg P/ha/yr) resulted in a population of VA mycorrhizal endophytes in Western Australian pasture soils that was little affected by subsequent additions of P (0 to 224 kg P/ha/yr for 10 yr) (31). Although slightly more spores were found at intermediate levels of P, neither the relative abundance of different spore types nor infection levels were consistently related to P applications. In glasshouse experiments with this soil, endophytes from plots given the highest rates of superphosphate (224 kg/ha) did not differ from those from plots given no P in their ability to infect and increase P uptake and growth of subterranean clover (ie, P-tolerant strains had built up during the previous 15-yr period of superphosphate additions).

There are instances of the annual crops acting selectively on the indigenous spore-forming endophytes. This was shown in detail by Schenck and Kinloch (38) in crops grown in monoculture for 7 yr on a newly cleared woodland site in Florida. There were more spores associated with soybean plants than with other crops and fewest spores in the original woodland soil. Three species of *Gigaspora* were most numerous around soybean roots, whereas two *Glomus* species were most prevalent with Bahia grass and *Acaulospora* spp. with cotton and peanuts. The largest number of mycorrhizal species was associated with sorghum. These findings contrast with results for naturally formed ecosystems in which there are few signs of host specificity (eg, none was detected between any of the six species of *Festuca* and 11 species of VA mycorrhizal fungi examined in western grasslands in the USA [25]).

The selective pressure exerted by plants on the soil mycorrhizal population may be toward greater infectivity rather than symbiotic effectiveness as Bowen (6) pointed out. The main exceptions to this would be plants that cannot grow adequately in a particularly P-deficient soil without an effective symbiosis, so that only those colonized by efficient endophytes will survive (eg, *Stylosanthes* spp. in low-P tropical soils [28] and species with seedlings that must become mycorrhizal to get established, such as in infertile





Figs. 1 and 2. 1, Portion of white clover root grown in peat and infected by the indigenous fine endophyte (IFE) and by *Glomus fasciculatus* 'E3.' Note the fine hyphae and tiny vesicles of IFE (top right) and the large vesicles of E3, each containing a characteristic single large oil globule (bottom left) (×225). **2,** Part of root cortex of white clover grown in peat and containing a mixed infection of **1,** indigenous fine endophyte with fine hyphae (IFE) and arbuscule subtended by fingerlike hyphae (A) (top half), and **2,** *Glomus fasciculatus* isolate E3 with large coiled hyphae and granular arbuscules (bottom half) (×575).

woodland soils [Fig. 3] [27]). Otherwise, if plant growth is reasonable irrespective of mycorrhiza, then the most infective, competitive endophytes would be favored and proliferate (eg, in fertile agricultural soils). Thus, competition between endophytes is an important ecological factor. The first to infect is likely to have most effect on the plant. In fact, the apparent inefficiency of some endophytes may merely reflect their slowness to infect.

Infectivity of VA mycorrhizal fungi may also be affected by plant breeding programs. For example, crop cultivars bred for resistance to pathogens may also be more resistant to other fungi including mycorrhizal endophytes. Little is known about this subject. Possibly the mycorrhizal fungi would adapt genetically to cope with such changes because they are adapted to a wide range of host plants and more variation may arise by mutation, whereas many obligate pathogens have restricted host ranges and thus are intrinsically less broadly invasive.

Little work has been done to identify strain differences within a single morphological species of VA mycorrhizal fungus, but these may show adaptation to soil factors. Isolates of the same species from different climatic regions will very likely have different temperature optima for activity.

SYMBIOTIC ACTIVITY

The ever-increasing number of experiments on the influence of VA mycorrhiza on plant growth indicates that the greatest effects occur in infertile soils low in plant-available phosphate. This is because the major effect of a mycorrhiza is to improve phosphate uptake in such soils. Most evidence from ^{32}P-labeled soils (19,37) and other experiments indicates that the mechanism is primarily a physical one, the mycorrhizal hyphae being broadly analogous to extra root hairs (3), increasing the amount of root-soil contact and hence the volume of soil exploited by the mycorrhizal root. In a typical soil containing about 10^{-6}M orthophosphate in the soil solution (equivalent to about 0.03 ppm P) a phosphate-depletion zone of 1 mm or so develops around the root because the root absorbs phosphate ions much more rapidly than they can diffuse through soil to replenish the rhizosphere. The mycorrhizal hyphae extend several centimeters into the soil, absorb phosphate from this undepleted area, and translocate it directly back to the root and then via the appressoria to the fungus in the root cortex where it is transferred to the plant, largely via the arbuscules. This action bypasses the phosphate-depletion zone and overrides many direct physiological effects of VA mycorrhiza on phosphate uptake which are limited by the number of ions at the root surface. This physical mechanism loses its significance if enough phosphate fertilizer is added to soil so that P-depletion zones do not arise, and when non-nutritional effects of mycorrhiza are implicated. However, if the soil is "phosphate-fixing" (eg, like the ferrolateritic types in the tropics) a plant may respond to mycorrhizal inoculation even after appreciable amounts of fertilizer have been added.

Increased removal of plant-available P from soil by VA mycorrhiza rather than release of some of the vast bulk of inert insoluble P (19,37) could lead to rapid exhaustion of the soil P reserves. Therefore, some fertilizer phosphate must be added for long-term maintenance of residual P. Recent experiments suggest that plants may more efficiently use small dressings of soluble superphosphate or sparingly soluble forms of P such as rock phosphate when they are mycorrhizal (28). Perhaps the chief agricultural benefit of mycorrhizal inoculation may lie in improving crop plant utilization of applied phosphate fertilizers.

The efficiency of the VA mycorrhizal symbiosis is affected by interactions between, and compatibility of, its three components: the fungal endophyte, the host plant, and the soil. Concerning the fungus, there is now considerable evidence of soil-endophyte specificity, as first shown in detail by Mosse (26), and some evidence of host-endophyte specificity.

Plants vary greatly in degree of dependence on VA mycorrhiza. This is governed chiefly by a plant's demand for and ability to take up phosphate from soil. As a broad generalization, crop plants such as wheat that have extensive fine root systems that provide a substantial soil-root interface are not likely to respond to introduction of a mycorrhiza-forming fungal associate, except in rather P-deficient soils. Others with coarser, less hairy roots such as onions, citrus, and *Stylosanthes*, are very responsive to mycorrhiza even in soils containing moderate levels of soluble P.

One example of the interaction between plant and soil affecting the mycorrhizal response is that of alfalfa/lucerne and *Stylosanthes* grown in a range of soils (*unpublished*). In a soil containing 8 ppm $NaHCO_3$-soluble P, mycorrhiza increased both growth and shoot percent P of alfalfa, but only increased percent P in the shoot in a soil containing 26 ppm P and increased neither percent P nor plant growth in soil with 40 ppm P. In the same 40-ppm-P soil, *Stylosanthes guyanensis* responded considerably to mycorrhiza, which is surprising in view of the success of *Stylosanthes* in tropical soils containing 2–3 ppm P and suggests that the plant may be obligately mycorrhizal under field conditions.

When the roots of different plant species intermingle in soil, mycorrhiza can affect plant growth differently. Two well-known examples are: similar uptake of soil P by the grasses *Holcus lanatus* and *Lolium perenne* in the absence of mycorrhiza, but increased and decreased uptake in *Holcus* and *Lolium*, respectively, with mycorrhiza (11); and *Trifolium repens* only able to compete with *Lolium perenne* in moderately P-deficient soil if mycorrhizal inoculum was added (9). Interspecific transfer of P may occur via interconnecting mycorrhizal hyphae in the soil, but this is difficult to prove experimentally (22).

Although virtually any VA mycorrhizal plant species can be infected to some extent by any VA mycorrhizal fungal species, the symbiotic interaction may differ for different host-fungus combinations. More important in endophyte specificity, however, is the suitability of the soil. For example, *A. laevis* and *G. fasciculatus* E3 are best in acid soils, but *G. mosseae* is best in neutral-alkaline soils. Too high a soil pH may inhibit the activity of E3 hyphae in soil, even when the fungus is well established inside the root. Waterlogging of soil may suppress mycorrhizal function due to insufficient oxygen for the fungus.

From Powell's (32) experiments with ^{32}P-labeled soils, it seems that different endophytes utilize the same source of soil P. Differences in their symbiotic effectiveness may be more related to arbuscule activity and nutrient exchange because there is not always a direct relationship between endophyte effectiveness and the amount of mycelium it produces in the soil around the root. Possibly the spacing of this external mycelium in soil is more critical than the total amount.

VA mycorrhizal fungi can enhance the uptake of other relatively immobile ions in soil besides phosphate. Zinc has been studied the

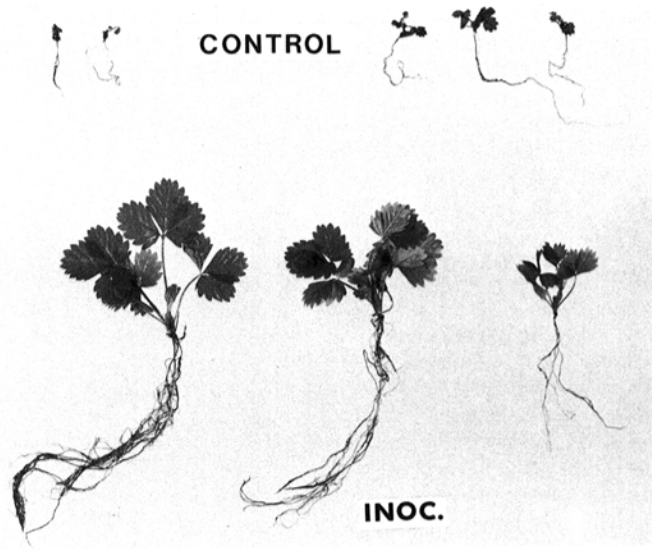


Fig. 3. Strawberry seedlings growing in a woodland soil (Meathop Wood) in which they occur naturally. The soil was sterilized by γ-irradiation and the plants grew poorly (CONTROL) unless reinoculated with the indigenous mycorrhizal fungi (INOC.).

most; mycorrhiza improves its uptake by peach in Zn-deficient soils in California (13). VA mycorrhiza may also increase the uptake of copper, sulphur, and cadmium from soil. Conversely it is speculated that mycorrhiza may increase plant tolerance of aluminum and manganese; both of these metals can reach toxic levels in some tropical soils. VA mycorrhiza does not affect uptake of N from soil, although it can enhance N_2-fixation by legumes in low-P soils indirectly by increasing P uptake (28).

We have seen that high soil fertility can preclude mycorrhizal benefits. In some soils, this effect may go so far as to tilt the host-endophyte balance from mutualistic symbiosis to parasitism. For example, Crush (8) showed growth inhibition in some grasses by *Rhizophagus tenuis* in a soil containing 8 ppm available P (by the Truog analysis technique) although the fungus enhanced growth in soil containing 4 ppm P. He also showed an unfavorable effect of some endophytes on certain pasture legumes at high levels of added superphosphate, implying that any practical mycorrhizal inoculation program in such soils must employ endophytes carefully selected for performance at realistic P levels (10). Nevertheless, Jensen and Jakobsen (23) showed that the symbiotic balance may not be so easily upset in various Danish agricultural soils containing a range of plant-available P and growing wheat and barley. They found no differences in shoot P content under practical field conditions, a low level of soil P apparently being offset by higher mycorrhizal infection and vice versa. Their results suggest the symbiosis is self-regulatory and that indigenous VA mycorrhizal fungi may be beneficial to the phosphate nutrition of cereals in low P soils rather than deleterious at high P levels. Furthermore Strzemska (41) showed that large applications of fertilizer that markedly decreased mycorrhizal infection did not increase yields of cereals or beans; this suggests, but does not prove, a balance between mycorrhiza and soil fertility.

From these various reports it can be seen that the indigenous soil population of VA mycorrhizal endophytes may or may not be effective in stimulating growth of a crop species in a particular soil. Figures 3 and 4 give two examples. Sometimes the indigenous population may be effective, but the initial inoculum density is too low for infection to build up fast enough to affect the early growth of a plant. At other times, even though the endophytes establish extensive infection, they have little effect on plant growth. Thus, composition of the indigenous endophytes is important both quantitatively and qualitatively.

Finally, the soil microflora also affects the functioning of the VA mycorrhizal system by acting on the nutrient-translocating external mycelium. Some soil microorganisms may suppress this mycelium directly or compete with it for soil nutrients, including phosphate. Others, by contrast, may act synergistically with the VA mycorrhizal fungi in their combined effects on plant growth; eg, the phosphate-solubilizing bacteria (2).

The large influence of soils and soil fertility on the ecological and symbiotic activity of VA mycorrhizal fungi is a major consideration in attempts to harness these fungi to our advantage. In general, benefits from mycorrhiza are most likely where efficient, specifically adapted endophytes infect crops with coarse root systems with a high demand for phosphate and that are growing in infertile soils containing either few or ineffective mycorrhizal endophytes.

Fig. 4. White clover seedlings growing in unsterile peat from a hill grassland site in mid-Wales. Both sets of plants were infected by the indigenous mycorrhizal fungi, but these were ineffective (cf, CONT.); only those inoculated with effective mycorrhizal fungi indigenous to a nearby hill grassland site (+4) grew well. All pots had received superphosphate (SP) at a rate equivalent to 40 kg P/ha.

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