# Mycorrhizae of nitrogen-fixing legumes

## D. S. Hayman

*Rothamsted Experimental Station, Harpenden, Hertfordshire, U.K.*

### Introduction

The mutualistic symbioses known as mycorrhizae are formed between certain soil fungi and the roots of most plant species. The plant partner benefits from improved uptake of nutrients, especially phosphate, and the fungus has a ready supply of carbon (photosynthate). It is not surprising, therefore, that mycorrhizal associations are found in almost all plant habitats and throughout the plant kingdom. They are common in plants that also enter into symbiotic partnerships with micro-organisms that fix atmospheric nitrogen within root nodules, namely bacteria (*Rhizobium*) in legumes and actinomycetes (*Frankia*) in certain non-legumes. The tripartite mycorrhiza–legume–*Rhizobium* symbiosis is the subject of this review.

It is normal for legumes growing in both uncultivated and agricultural soils to form mycorrhizae. Many legumes are extensively colonised by mycorrhizal fungi and some appear to be obligately mycorrhizal under natural conditions. By contrast, a few are only lightly infected and derive little or no benefit from the fungi. Between these two extremes lie most crop legumes, both forage and grain, of which the majority are fairly responsive, especially in soils where an insufficiency of plant-available phosphate limits growth. This in turn limits nitrogen fixation, which is dependent on adequate P levels within the plant. Hence the influence of mycorrhiza on legumes is potentially greater than for other plant groups because, by alleviating P-stress, the symbiotic fungi indirectly enhance the N-status of the legume. This leads to improved plant growth, and in some instances, increased protein content has been reported. Applied studies with legume mycorrhizae, therefore, have important global impacts, especially in cropping systems where inputs of P and N fertilizer are limited by economic constraints and shortfalls in supply.

### The host plants

The family Leguminosae contains 650 genera and 18,000 species (Polhill & Raven 1981), making it the third largest family of flowering plants. It is conventionally divided into three distinct sub-families (Allen & Allen 1981), mainly according to differences in floral structure. The sub-families Mimosoideae and Caesalpinoideae, consisting primarily of trees, shrubs and vines but few herbs, contain many species that are valuable as ornamentals or for their timber, dyes, resins and medicinal

properties. They are especially abundant in tropical rainforests, where they may account for half the trees present and are probably fixing vast quantities of nitrogen. The third sub-family, Papilionoideae, contains many species of agricultural importance in temperate and tropical regions. They are a highly nutritional food source for humans and animals, and are also useful as a ground cover in plantations and on eroded soils, and as green manures. Thus the family Leguminosae is second only to the Gramineae in economic importance.

Legumes show great variation in size, from large trees to small herbaceous ephemerals. They also range through virtually all terrestrial habitats and a diversity of climates. Hence they are of great importance not only in standard agricultural systems but also in marginal lands which are being exploited as pressures for land use expand around the world. In this, their ability to form dual symbioses which enhance their nutrient status is invaluable.

Mycorrhizal nitrogen-fixing legumes include many important temperate and tropical crops, e.g. clover, lucerne (alfalfa), beans (*Phaseolus* and *Vicia*), peas, soybeans, cowpea, pigeonpea, chickpea, groundnuts, *Stylosanthes*, *Pueraria* and *Centrosema*. These forage and grain legumes form endomycorrhiza of the vesicular–arbuscular (VA) type, as do most species in the Mimosoideae and Papilionoideae groups. Some arborescent legumes, e.g. *Leucaena*, also form VA mycorrhiza but many, especially in the Caesalpinoideae, form mycorrhiza of the ecto- type. In addition, certain leguminous shrubs, e.g. *Acacia*, have both ecto- and VA mycorrhiza. Table 1 gives a summary of the main legumes in which a mycorrhizal association has been reported. This list is inevitably selective because of the enormous number of legume species, many of which have not yet been investigated.

Nodulation by *Rhizobium* is fairly general in the Mimosoideae and Papilionoideae, but seems to be uncommon or sporadic in the Caesalpinoideae.

## The microbial symbionts

### Rhizobium

*Rhizobium* bacteria are common soil inhabitants, distinguished from other genera of soil bacteria by their ability to nodulate leguminous plants and fix nitrogen in the nodules. Different species are recognized by their physiological characteristics and by which legume groups they infect.

Nodulation can only occur when compatible rhizobia are present in the legume rhizosphere. Moreover, certain legumes are unable to nodulate at all. When nodulation is achieved, its effectiveness varies according to host and bacterial genotypes. This has led to the establishment of cross-inoculation groups that reflect the degree of specificity involved (see Allen & Allen 1981). Thus, particular strains of rhizobia are usually able to nodulate plants only within a specific group of legumes, e.g. *R. japonicum* on soybean. Also, ineffective nodules may result when rhizobia that produce effective ($N_2$-fixing) nodules on one legume species infect a related species.

Nodule effectiveness is also influenced by environmental factors. It is retarded by poor illumination (causing less photosynthesis) and by water stress and soil acidity (<pH 5). Activity of the enzyme nitrogenase, which is involved in $N_2$-fixation, is also dependent on an adequate supply of the trace elements Mo, Cu and Co. If the soil is reasonably rich in nitrogen, the rhizobia will tend not to nodulate—hence the need for a balanced approach (cf. parallels with mycorrhiza and phosphate) to utilizing the *Rhizobium*-legume symbiosis in crop production.

**Table 1**   Important legumes reported to be mycorrhizal

| Legume subfamily | Type of mycorrhiza in (genus) | |
|---|---|---|
| | ecto | VA |
| Caesalpinoideae | *Afzelia* | |
| | *Aldina* | |
| | *Anthonata* | |
| | *Bauhinia* | |
| | *Brachystegia* | |
| | *Cassia* | |
| | *Eperua* | |
| | *Gilbertiodendron* | |
| | *Julbernardia* | |
| | *Monopetalanthus* | |
| | *Paramacrolobium* | |
| | *Swartzia* | |
| Mimosoideae | *Acacia* | *Acacia* |
| Papilionoideae | *Bartonia* | *Aeschynomene* |
| | *Brachysema* | *Arachis* |
| | *Chorizema* | *Astragalus* |
| | *Daviesia* | *Cajanus* |
| | *Dillwynia* | *Centrosema* |
| | *Eutaxia* | *Cicer* |
| | *Hardenbergia* | *Cytisus* |
| | *Jacksonia* | *Desmodium* |
| | *Kennedya* | *Glycine* |
| | *Mirbelia* | *Hedysarum* |
| | *Oxylobium* | *Lathyrus* |
| | *Platylobium* | *Leucaena* |
| | *Pultenaea* | *Lotus* |
| | *Robinia* | *Medicago* |
| | *Vicia* | *Phaseolus* |
| | *Viminaria* | *Pisum* |
| | | *Pueraria* |
| | | *Trifolium* |
| | | *Stylosanthes* |
| | | *Vicia* |
| | | *Vigna* |

Partly from Harley & Smith 1983

*Mycorrhizal fungi*
Fungi that can form mycorrhizal associations with plants are found in all four major fungal classes (Basidiomycetes, Ascomycetes, Phycomycetes and Fungi Imperfecti). Likewise species in the main plant classes (Angiosperms, Gymnosperms, Pterido-phytes and Bryophytes) can become infected by mycorrhizal fungi. This straddling of taxonomic barriers suggests the mycorrhizal condition has evolved several times. Thus, unlike the *Rhizobium* symbiosis, mycorrhizal symbioses are virtually non-specific as the same fungus can infect a wide range of legumes and non-legumes. It is not surprising, therefore, that several fungal species can be mycorrhizal with legumes.
   Many (>1000) Basidiomycetes and some Ascomycetes form ectomycorrhiza on

trees and shrubs. The three other main types of mycorrhiza are grouped together as endomycorrhiza, but are not related. One is restricted to orchids and involves certain Fungi Imperfecti, one is confined to the Ericales in which one Ascomycete and possibly a Basidiomycete have been implicated, whereas the third, termed vesicular–arbuscular (VA) mycorrhiza, is found in most plant families and is formed by nearly 100 species of the family Endogonaceae (Phycomycetes–Zygomycetes) (Trappe 1982). Most plants are mycorrhizal and around 95% of all mycorrhizal plant species are believed to have the VA type (Meyer 1973). These include most crop families except the Cruciferae and Chenopodiaceae. VA mycorrhizal fungi are cross-compatible between the major crop families including the Gramineae, Leguminosae, Solanaceae, Rosaceae, etc. Many ectomycorrhizal fungi also infect across family boundaries.

Mycorrhizal fungi infect primarily the fine rootlets of a plant. They do not penetrate the vascular tissue and are absent from roots which no longer have a primary cortex. Ectomycorrhizal rootlets of woody plants are characterized by being shorter and thicker than non-mycorrhizal rootlets, partly due to the mantle of fungal mycelium encasing them. They vary in colour, form rhizomorphs (hyphal cords) which extend into the soil, and are large enough to be visible to the naked eye. Ectomycorrhizae are also characterized microscopically by the presence of intercellular hyphae and a Hartig net (hyphal network between the epidermal cells). VA mycorrhizae, by contrast, form no sheath but rather a network of loose hyphae in the soil around the roots. Also VA mycorrhizal infections are only distinguishable by differential staining and microscopic observation of the diagnostic fungal structures—vesicles, arbuscules, hyphal coils and intra- as well as intercellular hyphae. These VA mycorrhizal structures are typically found in herbaceous legumes.

The major role of mycorrhizal fungi in aiding plant nutrition, mainly by improving phosphate uptake, together with their other effects on plant growth, interactions with disease organisms and rhizobia, and ecophysiological considerations, will be discussed in the rest of this review in relation to current work on mycorrhizae in legumes. The emphasis will be on VA mycorrhiza and its significance in cultivated legumes, because of its implications in applied microbiology and biotechnology and because of the extensive literature on VA mycorrhizae in $N_2$-fixing leguminous plants.

### Factors affecting mycorrhizal infections in legumes

VA mycorrhizal fungi are among the most common soil fungi and probably infect more plant tissue than any other fungal group (Gerdemann 1968). In natural ecosystems more than half the feeding part of the root system of most plants, including legumes, can be infected. This is also the case in cultivated soils, except that infection can be drastically reduced by amendments with agrochemicals and by fallow periods or rotation with non-mycorrhizal crops.

The negative effect of phosphate fertilizer on VA mycorrhiza in crops is well known and is as true for legumes as for other plant species. For example, VA infection of white clover by indigenous endophytes in an upland pasture was decreased from 54% root length infected to 37% by the addition of superphosphate at 90 kg P/ha (Hayman 1984). Higher levels of P decrease infection even further, mainly through an increased P concentration in the plant tissues (Sanders 1975). However, VAM fungi vary in their sensitivity to phosphate. Relatively P-tolerant populations can build up in soil amended with P for many years and maintain moderately high infection levels, as

shown for subterranean clover (Porter *et al.* 1978), and many other legumes (Crush 1975).

Nitrogen fertilizer has a negative effect on VAM populations in many crops. Although this effect has been reported for groundnuts (Porter & Beute 1972), it is less consistent for legumes than non-legumes. For example, although N fertilizer depressed VAM spore populations and infection in field-grown wheat, it had little effect on nearby *Vicia faba* (Hayman 1975) or on other legumes (Strzemska 1975). There is now evidence that N acts more through the plant than the soil, e.g. Wang & Hayman (1982) noted a significant inverse correlation between %N in plant tissues and %VAM infection in onion and clover. The applied nitrogen was less inhibitory of infection percentage in the legume, apparently because it only affected N concentrations in the non-legume. Generally, the ammonium form of nitrogen is more inhibitory than the nitrate form (Chambers *et al.* 1980).

It is not surprising that fungicides and fumigants used to control soil-borne pathogens also kill or inhibit mycorrhizal fungi (see Menge 1982). This has important consequences for mycotrophic leguminous crops that depend on becoming infected by indigenous VAM fungi in order to make reasonable growth. Furthermore, even where VAM infection is not completely prevented by a fungicide, the infection may be unable to function and so fail to enhance plant growth, as shown in soybeans in soil drenched with benomyl (Bailey & Safir 1978). Some insecticides also inhibit mycorrhizal infection, but certain nematicides increase it. The effects of herbicides have been little studied.

Mycorrhizal populations in field crop systems are also affected by season, VA infection percentage commonly reaching a maximum towards the end of the growing season. With field-grown *Phaseolus* beans and soybeans, Sutton (1973) noted an initial lag phase of 20–25 days, which was attributed to rapid root growth of the seedlings and the time required for spore germination, germ-tube growth and penetration of the host plant root. In the second phase, lasting 30–35 days, extensive mycorrhizal development coincided with most shoot growth and copious spread of external mycelium, leading to multiple infections. During the third phase, from host fruiting to senescence, the proportion of mycorrhizal to non-mycorrhizal roots remained constant. Under some field conditions, the infection plateau in legumes is reached sooner, e.g. in peas (Jakobsen & Nielsen 1983). In the latter case, the infection plateau was considerably higher in peas (75%) than in cereals (50%) grown in the same field (Fig. 1).

Studies with plants grown in pots have shown a strong influence of environmental factors on VAM infection. Generally, high temperatures and light intensities increase infection, both in legumes and non-legumes. pH optima vary for different VAM endophytes (Hayman & Tavares 1985) such that, unlike the *Rhizobium*-legume symbiosis,the establishment of mycorrhizal symbioses in legumes depends more on soil factors than on host species.

Another factor affecting VAM infection is plant genotype. There is now evidence of major differences in susceptibility to VAM infection between cultivars of the same crop species, e.g. lucerne (Lambert *et al.* 1980) and *Phaseolus* beans (Sutton 1973). This should be considered in plant breeding programmes. It should also be taken into account in field inoculation trials and in crop rotations where soil populations of mycorrhizal fungi can build up under mycotrophic crops and so benefit a subsequent crop.
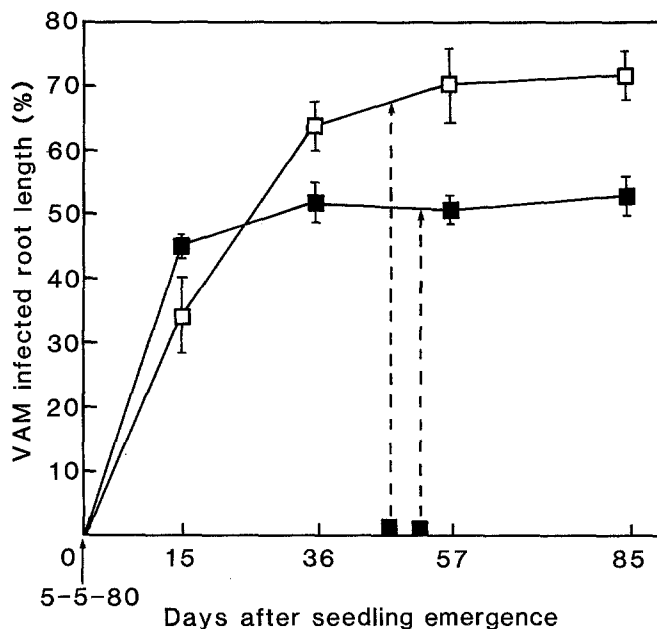
**Fig. 1** VAM infection in roots from the upper 15 cm of soil of spring barley (mean of 8 cultivars) (■) and peas (□) at various times after seedling emergence. Times of earing in barley and flowering in peas are indicated on abscissa; bars indicate S.E. (from Jakobsen & Nielsen 1983).

Finally, there have been attempts to represent the spread of VAM infection in young plants by the use of mathematical models, the chief example for legumes being *Trifolium subterraneum*. The model proposed for *T. subterraneum* by Walker and Smith (1984), and which presumably applies also to non-legumes, incorporates two major processes that determine the amount of root infected: '(1) the encounters between roots and external hyphae that lead to the initiation of new infection units by means of entry points in the epidermis; (2) the increase in length of infection units by mycelial growth within the cortex'. This model underlines the importance of propagule density, which has also been demonstrated experimentally, e.g. for *Trifolium repens* (Jensen 1984). Thus, provided propagules occur randomly in the soil, the rate of initiation of new infections is proportional to propagule density over short periods (5–11 days). However, the wide range of biological and physico-chemical factors that influence the infectivity of different endophytes and the susceptibility of plant tissues, as described above, illustrate the difficulties at present of applying models to field situations.

## Components of the legume–mycorrhiza symbiosis

It is difficult to grade the responsiveness of legumes to mycorrhizal infection, based on reports in the literature. This is partly because the P-status of the soil, as well as endophyte species/strain and plant species/cultivar, affects the end result of the symbiosis. In other words, the mycorrhizal symbiosis is not solely a plant–micro-organism interaction, but rather a three-way interaction involving the soil as well. Work on legumes amply illustrates the roles of the three components.

## The Soil

Soil fertility is a key factor. Often the chances of a growth response to mycorrhiza can be predicted from analyses of plant-available soil P, as commonly estimated by the Olsen test (Olsen *et al*. 1954) using $NaHCO_3$ as an extractant. Thus gross, but not exact, inverse correlations have been reported between Olsen P levels and plant response to mycorrhiza. This is exemplified with lucerne (Hayman 1983), where VA mycorrhiza increased both growth and shoot %P in soil containing 8 ppm Olsen P, increased %P but not growth in soil with 26 ppm P, and increased neither in soil with 40 ppm P (Table 2). Such experiments must be done in soils which have been sterilized in order to have non-mycorrhizal controls, although applied inoculation studies must ultimately be done against the background of the native soil VAM population.

**Table 2** Effect of mycorrhiza on growth and P content of lucerne grown in soils of different P fertility

| Soil P content[*] | Shoot dry weights (g) | | %P in shoot | |
|---|---|---|---|---|
| | myc | non-myc | myc | non-myc |
| 8 | 1.03 | 0.03 | 0.17 | 0.09 |
| 26 | 3.15 | 2.46 | 0.16 | 0.08 |
| 40 | 4.53 | 3.39 | 0.18 | 0.18 |

[*] ppm soluble in $NaHCO_3$ (Olsen *et al*. 1954)
Hayman, unpublished

## The Plant

The different extent to which different legume species depend on mycorrhiza is well illustrated by experiments showing doubling of growth of *Stylosanthes guyanensis* by VAM in the same 40 ppm P soil in which the normally mycotrophic lucerne was no longer responsive (Hayman 1983). Paradoxically, *Stylosanthes* spp can grow successfully in tropical regions in soils containing less than 3 ppm Olsen P, which suggests it is highly dependent on becoming infected by the native mycorrhizal fungi. Islam *et al*. (1980) reported that inoculation with VAM fungi doubled growth of cowpeas but did not affect soybeans growing in the same soil.

   Root geometry can largely explain why certain plants are mycorrhiza-dependent (Baylis 1972). As a broad generalization crop plants like wheat, which have extensive, fine root systems that provide a large soil–root interface, are less mycotrophic than plants with coarser, less hairy roots, e.g. onions, citrus and *Stylosanthes*. Other factors must also be involved, however, as not all plants fit this scheme. Within the legumes, Crush (1974) has shown an inverse relationship between mycotrophy and root hair development, *Lotus pedunculatus* (root hairs long and many) being less mycorrhiza-dependent than *Trifolium repens* (root hairs short and few) and especially *Centrosema pubescens* and *Stylosanthes guyanensis* (root hairs short and sparse) (Table 3). Similarly *Leucaena leucocephala*, a leguminous tree with virtually no root hairs, is strongly mycotrophic (Munns & Mosse 1980). Thus the extra-radical VAM fungal hyphae are broadly analogous to extra root hairs, increasing physically the volume of soil exploited for nutrients. However some lupins without abundant root hair development seem to be almost devoid of mycorrhiza, yet are still able to obtain

**Table 3**   Effects of mycorrhiza and phosphate on growth and nodulation of four legumes in a sterilized, low-phosphate soil

| | Total fresh weight (g) | | | Nodulation[†] | | | Roots with root hairs (%) | Hair length (μm) |
|---|---|---|---|---|---|---|---|---|
| | M[*] | NM[*] | P[*] | M[*] | NM[*] | P[*] | | |
| *Centrosema pubescens* | 3.9 | 1.7 | 4.9 | 5 | 1 | 5 | 17 | 106 |
| *Stylosanthes guyanensis* | 1.6 | 0.5 | 0.9 | 5 | 0 | 5 | 6 | 108 |
| *Trifolium repens* | 2.6 | 1.6 | 4.0 | 5 | 1 | 5 | 79 | 213 |
| *Lotus pedunculatus* | 2.0 | 2.5 | 3.9 | 4 | 4 | 5 | 99 | 809 |

[*] M, + Mycorrhiza, NM, nil, P, + phosphate (0.4 g $Ca(H_2PO_4)_2.H_2O$/kg soil)
[†] Nodulation category: 0 (no nodules) to 5 (abundant nodules)
After Crush 1974

phosphate from infertile soil—this may be due to the proteiod root structures reported on some species (Trinick 1977).

*The Fungus*
Species and strains of ecto- and VA mycorrhizal fungi vary greatly in their infective potential and symbiotic effectiveness. Factors involved are their preferences for particular soils and host plants ('specificity'), innate effectiveness at stimulating plant growth, competitive ability in soil, and tolerance to added fertilizers and pesticides. The amount of root infected is not necessarily an indication of the endophyte's ability to enhance plant growth.

Although some plant–fungus combinations may be relatively ineffective, virtually any VAM plant species can be infected to some extent by any VAM fungal species. There is, however, some specificity in the effectiveness of the interaction. For example, Oliveira & Lopes (cited by Lopes & Siqueira 1981) showed *Glomus macrocarpum* to be effective on both grasses and legumes, whereas *Gigaspora margarita* and *Acaulospora laevis* were effective only on the grasses tested. Also *Glomus epigaeum* was less effective than *Glomus mosseae* and *Glomus* E3 on two varieties of *Vigna unguiculata* (Olivier *et al.* 1983). Nevertheless, the suitability of the soil is a more important determinant of specificity (Mosse 1973). Thus some fungi are only effective in acid soils, whereas others are better in neutral to alkaline soils, and certain ones have a broad soil pH tolerance. In addition, different endophytes have different temperature optima (Schenck & Smith 1982).

An example of differences between endophytes is that reported for groundnuts and soybean, which developed more VAM infection when inoculated with *Glomus* plus *Gigaspora* than with *Glomus* alone (Ross & Ruttencutter 1977). Numbers of *Glomus* chlamydospores formed in the soil increased rapidly following field inoculation by this fungus alone but not when *Gigaspora* was included. This was attributed either to its poor competitive ability relative to *Gigaspora* or to specific hyperparasites.

**Effects of mycorrhiza on legume growth**
Published experiments on the effects of mycorrhiza on legume growth are far too numerous to cite here. Most illustrate the often dramatic effects of mycorrhizal fungi

on plant uptake of phosphate and consequently plant growth. In addition, mycorrhizae influence the uptake of certain other nutrients and water and also affect the physiology of the host plant.

*Phosphate*

The major visible benefit of mycorrhiza to plant growth is via phosphate nutrition because P is a major plant nutrient and P-deficient plants are usually stunted. As P-deficient soils are often low in nitrogen also, inoculation tests with mycorrhiza on $N_2$-fixing legumes have been particularly prominent. Table 4 gives some examples. Indeed, at the recent 1st European Symposium on Mycorrhizae (Dijon, France, 1–5 July 1985), all the papers on practical aspects of VAM were concerned with legumes or cassava (also a highly mycotrophic crop).

According to the evidence from experiments in $^{32}$P-labelled soils, in which mycorrhizal and non-mycorrhizal plants took up P with the same specific activity ($^{32}$P/total P), irrespective of differences in total P uptake and plant size, mycorrhizal plants absorb phosphate from the same labile pool as non-mycorrhizal plants (Hayman & Mosse 1972; Sanders & Tinker 1973; Gianinazzi-Pearson *et al*. 1981). They do not appear to tap additional sources of native soil P, e.g. by dissolving insoluble forms of P. This conclusion is supported by other experiments, e.g. with mycorrhizal and non-mycorrhizal soybeans fed different forms of inorganic P (Ross & Gilliam 1973). From these results, it is deduced that the mechanism for increased P uptake by plants that are mycorrhizal is primarily a physical one. Thus the mycorrhizal hyphae are believed to absorb extra P from the labile pool beyond the P-depletion zone. This zone coincides approximately with the rhizosphere, and develops in low-P soils because the roots absorb phosphate ions much faster than the ions can be replenished at the root surface by diffusion through soil. The fungal hyphae can extend several centimetres from the root and directly translocate P into the root cortex. There it is transferred to the plant, probably mainly via the arbuscules.

The physical mechanism largely accounts for the most mycotrophic plants generally having root systems with poor root hair development (see page 127), because the hyphae are somewhat analogous to extra root hairs. Clearly this mechanism is vital to the plant in P-deficient soils, but it no longer operates when enough P fertilizer is added that diffusion through soil is no longer a limiting factor. Nevertheless, in highly 'phosphate-fixing' soils such as in the tropics, large applications of P fertilizer may not preclude responses to mycorrhiza.

The greater benefit of mycorrhiza to the P nutrition of some legumes compared to certain other plant species can affect plant competition and survival in mixed plantings. For example white clover grew poorly relative to ryegrass in a sterilized low-P soil, whereas in the presence of either added P or mycorrhiza clover growth was greatly improved while the ryegrass was unaffected (Table 5, Crush 1974).

The balance of P in the mycorrhizal system is important. To some extent the symbiosis is self-regulatory, large amounts of applied P decreasing infection which is no longer needed for P uptake. However, at very high levels of applied P, the fungus may occasionally have a negative effect on plant growth, as shown by Crush (1976) with some endophytes on certain pasture legumes in New Zealand.

It is well known that in some tropical soils P-deficiency may be even more important than N-deficiency as a factor that limits plant growth. For example Cornet & Diem (cited by Gianinazzi-Pearson & Diem 1982) found that seedlings of *Acacia*

**Table 4** Major growth experiments on mycorrhizal inoculation of legumes (selected)

| Legume species | Reference |
| --- | --- |
| *Acacia farnesiana* | Johnson & Michelini 1974 |
| *Acacia raddiana* | Gianinazzi-Pearson & Diem 1982 |
| *Arachis hypogaea* | Daft & El-Giahmi 1976 |
| *Centrosema pubescens* | Crush 1974 |
| | Mosse *et al.* 1973 |
| *Glycine max* | Asimi *et al.* 1980 |
| | Bagyaraj *et al.* 1979 |
| | Bethlenfalvay *et al.* 1981 |
| | Jackson *et al.* 1973 |
| | Ross 1971 |
| | Ross & Gilliam 1973 |
| | Ross & Harper 1970 |
| | Safir *et al.* 1971, 1972 |
| | Schenck & Hinson 1973 |
| | Schenck *et al.* 1975 |
| *Hedysarum boreale* | Redente & Reeves 1981 |
| *Leucaena leucocephala* | Munns & Mosse 1980 |
| *Lotus pedunculatus* | Crush 1974 |
| | Hall 1980 |
| *Medicago sativa* | Azcón-Aguilar *et al.* 1979 |
| | Owusu-Bennoah & Mosse 1979 |
| | Smith & Daft 1977 |
| *Phaseolus vulgaris* | Daft & El-Giahmi 1974 |
| | McIlveen *et al.* 1975 |
| *Pueraria phaseoloides* | Waidyanatha *et al.* 1979 |
| *Stylosanthes guyanensis* | Mosse 1977 |
| | Mosse *et al.* 1976 |
| *Trifolium repens* | Crush 1974, 1976 |
| | Hall 1984 |
| | Hayman & Mosse 1979 |
| | Powell 1977, 1982 |
| | Sparling & Tinker 1978 |
| *Trifolium subterraneum* | Abbott & Robson 1977, 1978 |
| | Barrow *et al.* 1977 |
| | Smith & Bowen 1979 |
| *Vicia faba* | Kucey & Paul 1982 |
| *Vigna unguiculata* | Islam *et al.* 1980 |
| | Ollivier *et al.* 1983 |
| Several legumes | Asai 1944 |
| | Crush 1976 |

*raddiana* failed to grow in a soil from Senegal unless mycorrhizal or given phosphate; then they grew well even though they were not nodulated. Similarly Mosse (1981) pointed out that lack of phosphate is the most important constraint to plant growth in many tropical soils. Responses to N will occur only after this P deficiency is overcome.

**Table 5** Response to mycorrhizal inoculation or phosphate fertilizer of *Trifolium repens* and *Lolium perenne* grown together in a sterilized, low-phosphate soil

|  | Total fresh weight (g) | |
|---|---|---|
|  | *Trifolium* | *Lolium* |
| + Mycorrhiza | 2.27 | 8.86 |
| Nil | 0.78 | 9.37 |
| + Phosphate | 3.44 | 9.14 |

After Crush 1974

Hence the ability of mycorrhiza to alleviate P-stress in such situations is doubly important.

*Nitrogen*

There is no evidence that mycorrhizal fungi fix atmospheric nitrogen. Also the fungi do not appear to increase the uptake of nitrate ions, except indirectly by virtue of producing larger plants. The ability of endomycorrhizal fungi to enhance uptake of ammonium ions and organic N in the Ericales (Stribley & Read 1980) has not been proved for other mycorrhizal groups. The main effect of mycorrhiza on plant nitrogen status is found in $N_2$-fixing plants. This is an indirect effect via an interaction with the rhizobial symbiont, and is discussed on pages 132–133.

*Trace Elements*

Mycorrhizal infection can help plant roots take up other ions besides phosphate which have low mobility in soil. Improved uptake of zinc by mycorrhiza has been shown in Zn-deficient soils for certain crops including pinto bean (McIlveen *et al.* 1975). Sulphur uptake by red clover grown in sand supplied with nutrient solution was also increased by VAM (Gray & Gerdemann 1973). Cooper & Tinker (1978) observed mean flux ratios of 50 : 8 : 1 for the transfer of $^{32}P$, $^{35}S$ and $^{65}Zn$, respectively, into mycorrhizal clover seedlings. Copper uptake may also be enhanced by mycorrhiza (Gildon & Tinker 1983), and mycorrhizal soybeans took up more radioactive strontium from solution than non-mycorrhizal plants (Jackson *et al.* 1973). By contrast, mycorrhizal infection did not alleviate molybdenum deficiency of *Phaseolus* beans growing in Mo-deficient soil (Hayman & Day 1978). As trace elements such as Zn, Cu and Mo are involved in nodulation or $N_2$-fixation, the role of mycorrhiza in their uptake by legumes is clearly significant. The balance between these trace elements and phosphate is important because a deficiency of these elements can arise in a plant where excessive applications of phosphate inhibit mycorrhizal infection. Conversely, too high levels of zinc inhibited mycorrhiza and nodulation in Pinto beans (McIlveen *et al.* 1975). Where boron levels in soil were marginal to plant growth, this was reported to be more deleterious to mycorrhizal than to non-mycorrhizal plants of red clover and lucerne (Lambert *et al.* 1980).

*Carbon*

Microsymbionts in roots obtain their carbon from photosynthesis by the plant. This is a potential drain on the host plant, which is compounded in legumes which support

both rhizobia and mycorrhizal fungi. Therefore the host plant must be compensated for this loss, i.e. in the form of enhanced nutritional status, otherwise it would have evolved immunity.

Light is obviously a limiting factor, and it has been shown that shading can decrease both root infection and the plant response to VA mycorrhiza (Nyabenda 1977; Moawad 1979; Hayman 1983). Conversely, the high light intensities in the tropics may favour symbiotic activity and account in part for the importance of rhizobia and VAM fungi in tropical legume crops.

Although there is some controversy over the significance of a carbon drain, work on source–sink relationships with legumes suggests a compensation mechanism. Thus in faba beans, Pang & Paul (1980) showed more $CO_2$ lost by respiration from mycorrhizal than non-mycorrhizal roots, but there was no effect on yield even though mycorrhiza did not increase $N_2$-fixation. Furthermore Kucey & Paul (1982) showed,also with faba beans, that any carbon drain could be offset by increased photosynthesis.

## Hormones

There is recent evidence that VA mycorrhiza affects the hormone balance in plants, e.g. cytokinins (Allen *et al.* 1980). Also the ability of VAM to overcome first-year dormancy in cuttings may be in part a hormonal effect (Kormanik *et al.* 1979). This topic does not appear to have been studied in legumes.

## Water

Currently there is much interest in whether mycorrhiza can relieve water stress in plants, particularly in drought areas. Certainly there is an indirect effect, as where VAM is reported to enable some plants to resist transplant shock. This includes studies with the arborescent legume *Acacia raddiana*, where leaflets of mycorrhizal seedlings remained open whereas those of the controls were closed, suggesting better control of evapotranspiration in the former (Gianinazzi-Pearson & Diem 1982). Another indirect effect was reported in soybeans where resistance to water transport was decreased by VAM infection (Safir *et al.* 1972); this was probably because the fungus improved the nutritional status of the plant because adding phosphate had the same effect.

Direct involvement of the fungal hyphae has been shown with ectomycorrhizal associations. Here the anatomical structure of the fungal rhizomorphs permits conduction of water (Duddridge *et al.* 1980). This is more difficult to demonstrate for the fragile network of VAM hyphae around roots, although Hardie & Leyton (1981) interpreted the 2- to 3-fold increase in hydraulic conductivity they measured in red clover roots when mycorrhizal to be mainly due to hyphal growth in the soil.

## Mycorrhiza–*Rhizobium* interactions

A major reason for the abundance of mycorrhizal studies with legumes is that nodulation and $N_2$-fixation by rhizobia require a high P status in the host, which can often be affected by the mycorrhizal endophyte. Thus the effects of VAM on legume growth and *Rhizobium* activity are usually similar to those of adding phosphate.

Asai (1944) was probably the first to demonstrate that several legumes grow poorly and fail to nodulate in sterilized soil unless they are mycorrhizal. Since then, this effect has been shown experimentally with various legumes including *Arachis hypogaea*

(Daft & El-Giahmi 1976), *Centrosema pubescens* (Fig. 2, Crush 1974), *Glycine max* (Ross 1971; Schenck & Hinson 1973; Carling *et al.* 1978), *Hedysarum boreale* (Redente & Reeves 1981), *Medicago sativa* (Smith & Daft 1977), *Phaseolus* sp. (Daft & El-Giahmi 1976; Hayman & Day 1978), *Pueraria* sp. (Waidyanatha *et al.* 1979), *Stylosanthes* sp. (Mosse 1977; Mosse *et al.* 1976; Waidyanatha *et al.* 1979), *Trifolium repens* (Hayman & Mosse 1979; Mosse *et al.* 1976), *Trifolium subterraneum* (Abbott & Robson 1977) and *Vigna unguiculata* (Islam *et al.* 1980). The importance of N × P interactions in legumes is emphasised by data showing that VAM improved growth of a nodulating but not of a non-nodulating soybean isoline (Schenck & Hinson 1973).

Utilization of added P fertilizer in the *Rhizobium*–VAM interaction is a vital area for practical studies, as this could increase the efficiency of the tripartite symbiosis. Also of practical importance is the evidence that mycorrhizal infection can lead to increased nitrogen content of shoots and seeds (Daft & El-Giahmi 1974; Ross 1971; Schenck & Hinson 1973). This is of fundamental significance for human nutrition and underlines the need for further studies on mycorrhizal effects on protein levels in legumes.

Although it is clear that the main effect of VA mycorrhiza on *Rhizobium* activity and nitrogen fixation is phosphate-mediated, virtually nothing is known about direct interactions between VA mycorrhiza and rhizobia. Hence the fact that nodulation and nitrogenase activities of *R. japonicum* can still be enhanced by VAM even at high levels of added P fertilizer (Asimi *et al.* 1980) should be studied further, as it suggests an effect beyond just better P nutrition. The fungi do not normally penetrate the nodule tissues, but may influence the rhizobia by altering the root or rhizosphere environment (Crush 1974). Conversely, the rhizobia may influence the mycorrhizal establishment by producing polysaccharide which leads to increased synthesis of polygalacturonase at the infection site (Azcón-Aguilar *et al.* 1980).

Serial harvests of lucerne showed that the effects of mycorrhiza on nodulation and nitrogenase activity preceded those on growth (Smith & Daft 1977; Smith *et al.* 1979). This suggests that the nodules had first call on the phosphate. Hence future studies on VAM–*Rhizobium* interactions should emphasize the dynamics of the system and measure not only total plant N at harvest, but also acetylene reduction during the course of an experiment.

The interaction of the two microsymbionts can sometimes increase plant growth substantially, as shown for *Stylosanthes guyanensis* grown in very P-deficient soil (2 ppm Olsen P) from the Brazilian Cerrado (Mosse *et al.* 1976). In these experiments, the combination of *Glomus* E3 and rock phosphate greatly increased nodulation and $N_2$-fixation, in addition to P uptake, whereas plants with neither E3 nor rock P remained stunted (Fig. 3).

Many strains of *Rhizobium* maintained in culture collections are adapted to media containing 100 times more P than is usual in the soil solution (Munns & Mosse 1980). They can require at least 0.1% P in the shoot tissues in order to produce nodules on the roots (Mosse *et al.* 1976). Some indigenous rhizobia in soil, on the other hand, can nodulate at lower concentrations of P to which they are adapted (Mosse 1977), an important consideration when selecting inoculants for dual inoculation of legumes in P-deficient tropical soils in particular.

**Mycorrhiza and disease tolerance**

The extensive literature on this topic (see Schenck & Kellam 1978) shows that the
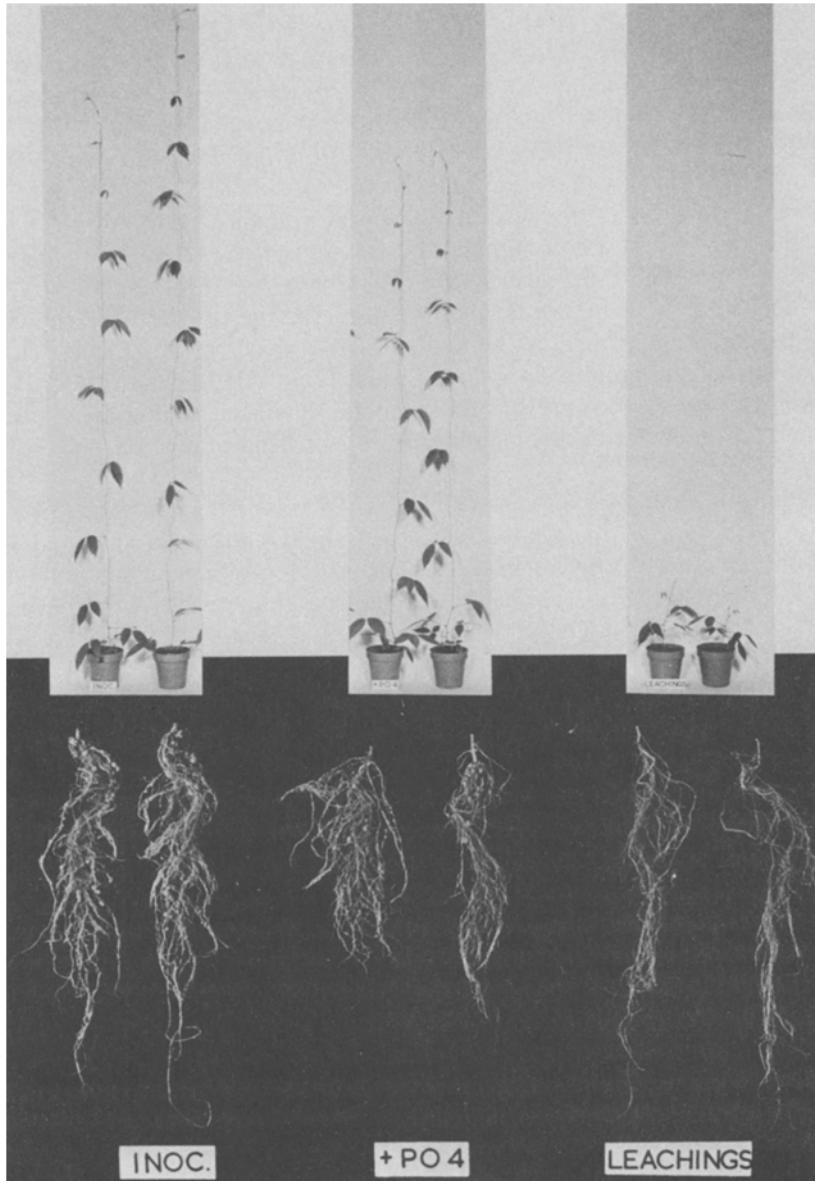
All plants inoculated with RHIZOBIUM

**Fig. 2** Effect of VAM on growth and nodulation of *Centrosema pubescens*. INOC = inoculated with *Glomus fasciculatum* E3; + PO$_4$ = Ca(H$_2$PO$_4$)$_2$H$_2$O applied at 0.4 g/kg soil; LEACHINGS = filtered washings of the E3 inoculum, containing contaminating microorganisms but not the VAM fungus itself. All plants were inoculated with *Rhizobium*. (from Crush 1974).

influence of mycorrhiza on fungal pathogens of plant roots varies with different diseases. Legume roots are no exception. In a detailed study with soybeans, Ross
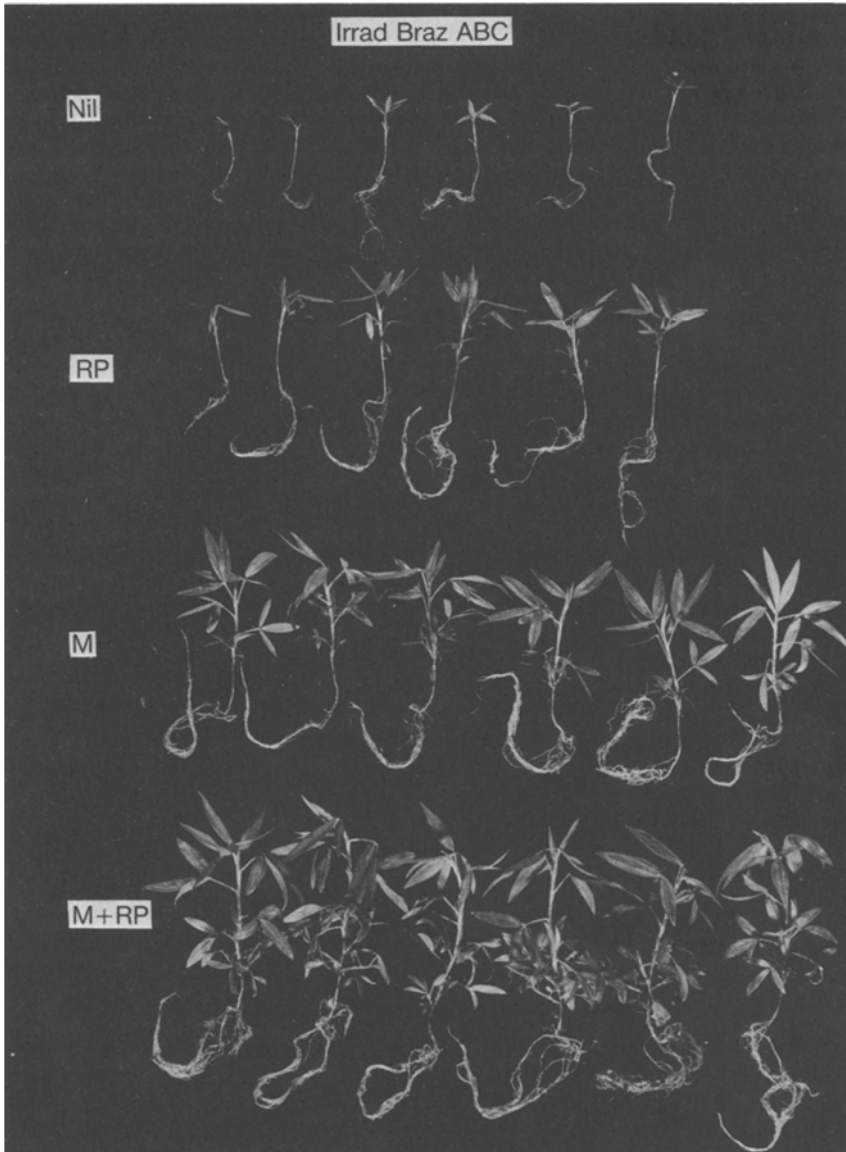
**Fig. 3** Growth of *Stylosanthes guyanensis* in a sterilized P-deficient Brazilian soil with and without mycorrhiza (M) (*Glomus* E3) and rock phosphate (RP). (from Mosse *et al.* 1976.)

(1972) found that VA mycorrhizal infection was associated with increased root rot by *Phytophthora megasperma* var. *sojae*. More frequently, there is no effect of VAM or VAM decreases disease expression. This last effect has encouraged belief in mycorrhizal fungi as possible biocontrol agents. However, if this is to become a reality, specific combinations must be evaluated individually as the protective

effectiveness of VAM varies with fungal and plant species/strain. In addition, VAM is most likely to protect plants against root disease if well established ahead of exposure to pathogens. This could be utilized for nursery transplants and should be tested with appropriate woody legumes. With ectomycorrhizal fungi, some protection has been shown by the mycelial sheath and the production of antibiotics (Marx & Krupa 1978).

Nematode–mycorrhiza interactions in legumes also range from negative to positive effects on the plant. Often nematodes and VAM fungi mutually suppress one another, probably due to competition for infection sites. Generally the beneficial effect of VAM does not fully compensate for the damage caused by nematodes, e.g. in *Vigna unguiculata* inoculated with *Glomus mosseae* and *Pratylenchus sefaensis* (Gianinazzi-Pearson & Diem 1982), although in some cases the harmful effect of the nematode is suppressed, e.g. by *G. mosseae* on *Scutellonema cavenessi* in soybeans (Germani *et al.* 1982).

## Practical considerations

### Fertilizers

Legumes are often grown with sub-optimal inputs of N and P fertilizers. Hence the ability of mycorrhiza to increase phosphate fertilizer utilization efficiency, and improve plant productivity at reduced levels of soluble P fertilizer or with alternative sources of P such as phosphate rock, is invaluable. In addition, the stimulation of $N_2$-fixation by mycorrhiza, even in the presence of P fertilizer, permits inputs of N fertilizer to be minimal (often applied as a small dressing of 'starter nitrogen' at the beginning of the growing season). Thus legumes, with a balanced mycorrhiza-*Rhizobium* symbiosis, are an indispensable component of sustainable agricultural systems in areas where over-reliance on fertilizers is impossible.

### Legume Type

As seen in earlier, both grain and forage legumes can respond to mycorrhizal infection. With forage legumes, this response is readily visible as increased growth and is important in diverse grass-legume grazing systems, legume ground cover in plantations, and pure legume stands grown for fodder. With grain legumes, increased growth is not necessarily correlated with improved grain yield or quality (including seed protein content), which must also be measured to evaluate the effectiveness of the mycorrhiza. Mixed cropping of legumes and non-legumes should be examined further where different crop species may share the same endophyte.

### Global

It is by now self-evident that legumes are vital to tropical agriculture where fertilizers are in short supply. Also many tropical soils are 'phosphate-fixing', i.e. have a very high sorption capacity for P, an effect which may not be reversible. The activity of micro-organisms such as mycorrhizal fungi is high at tropical temperatures and is enhanced by an ample supply of carbon from increased photosynthesis at high light intensities. Therefore there is considerable interest currently in field trials with legumes and mycorrhiza in the tropics, e.g. cowpea in Nigeria (Islam *et al.* 1980), Brazil (La Torraca 1979) and Senegal (Gianinazzi-Pearson & Diem 1982), and soybean in India (Bagyaraj *et al.* 1979) and Senegal (Gianinazzi-Pearson & Diem 1982).

Field experiments on legumes and VAM in temperate regions include those on

lucerne in England (Owusu-Bennoah & Mosse 1979) and Spain (Azcón-Aguilar *et al.* 1979), *Lotus pedunculatus* in New Zealand (Hall 1980), white clover in the UK (Hayman & Mosse 1979; Rangeley *et al.* 1982; Hayman 1984) and New Zealand (Powell 1977, 1982; Hall 1984), soybean in North America (Ross & Harper 1970; Schenck & Hinson 1973), and peas in the UK (Mosse *et al.* 1980).

### Inoculation techniques

Much has been written on this topic recently (see Hayman 1982; Schenck 1982; Menge 1983; Powell 1984). Therefore only a few relevant points need to be mentioned here.

One of the major problems with VAM studies is that the fungi cannot be grown in pure culture. They must be grown on stock plants ('pot cultures'). Consequently, VAM inoculum is rather bulky, and large quantities are needed to inoculate crops sown in the field. In fact, small-scale experiments have used the equivalent of around 2 t/ha (Hayman 1982). Currently the use of pellets (*ca.* 1 cm diameter), which contain inoculum in which the seeds are embedded, offers a practical means of introducing inoculum (VAM and *Rhizobium*) with seeds of small-seeded legumes and ensures that seedling roots are infected by the inoculants before exposure to the indigenous soil microflora. This is currently being tested on white clover in upland pastures (Hayman *et al.* 1986). Alternatively, inoculum is applied in pellets (Hall 1980) or in alginate beads (Diem *et al.* 1981) separately from the seeds, which could be useful for large-seeded legumes like soybean. Fluid drilling is also useful for legumes because both VAM and *Rhizobium* inoculants can be incorporated with the seeds in a slurry as shown with red clover (Hayman *et al.* 1981).

For legumes that can be transplanted to the field, pre-inoculation of seedlings in the nursery can be successful with far less inoculum. Also mycorrhizal infection can be established in these transplants in a sterilized compost free from competing native endophytes. This is in contrast to unsterile field soils where the effectiveness, competitive ability and abundance of native VAM fungi is a major determinant of the feasibility of introducing inoculants.

A corollary of introducing inoculants is manipulation of indigenous mycorrhizal populations by crop management procedures. When manipulation is not planned, as with side effects from crop protection chemicals, the hitherto unsuspected value of the indigenous mycorrhiza may become apparent.This aspect needs more appreciation, especially where mycotrophic crops such as many legumes are concerned.

### VAM inoculum

It is difficult to produce VAM inoculum in sufficient quantity and of adequate quality for field use. Currently it is produced on plants in large containers in glasshouses, protected against contamination by other VAM fungi or pathogens. Normally it is grown on a host unrelated to the crop to be inoculated to preclude any build-up of host-specific disease organisms. Thus inoculum for legumes is often grown on maize or sorghum. It is hoped that the biotechnology of mycorrhizal inoculant production will be further refined to facilitate attempts to capitalize on their plant growth-promoting potential under commercially acceptable conditions.

### Conclusions

The most important areas for present and future research on mycorrhizae of nitrogen-fixing legumes include:

(1) Legume mycotrophy—which species, and even which varieties within a species, benefit most from mycorrhiza; also why different genetic lines of plants behave differently in this respect.

(2) Possible importance of a carbon drain from host plant to the dual mycorrhiza-*Rhizobium* symbiosis in legumes.

(3) Environmental conditions that enhance mycorrhizal benefits to legumes.

(4) Increased fertilizer use efficiency by legumes when mycorrhizal.

(5) Specificity in legume–*Rhizobium*–VAM fungus interactions; selection of optimum combinations.

(6) Enhanced nodulation, $N_2$-fixation and protein levels in grain legumes.

(7) Improved establishment of forage legumes in pastures.

(8) Re-establishment of vegetation, with emphasis on legumes, in eroded or degraded sites and in semi-deserts.

(9) Re-introduction of VAM after soil sterilization.

(10) Better establishment of woody legumes by pre-inoculation of transplants.

(11) Introduction of VAM into *in vitro* vegetative propagation techniques for rapid reproduction of healthy, high quality plants for outplanting.

Indigenous VAM endophytes, adapted to local conditions, should be isolated and screened for these purposes. The best ones should be chosen and studied selectively in specific situations where benefits are judged to be most likely. They should be combined with elite strains of *Rhizobium* bacteria for dual inoculation of legumes. The ultimate assessments must be made realistically, i.e. in the context of the indigenous mycorrhizal fungi and rhizobia, both of which vary in their symbiotic efficiency. Inoculation of legumes, in conjunction with minimal N fertilizer and better utilization of less P fertilizer (rock or super), is being tested as a practical proposition in many countries.

With present technology, inoculation should be most successful with perennial and woody legumes where inoculum applied once in the field or transplant pots should survive for a few years with the crop. It is hoped that further investigations, fundamental and applied, especially in sustainable low-input cropping systems, will lead to improved utilization of the substantial potential of mycorrhiza in legume productivity.

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## Summary

Most plant species form mycorrhizae, which are symbiotic fungus-root associations. Many plants can also form symbioses with specific bacteria or actinomycetes which produce root nodules and fix atmospheric nitrogen within these nodules. The tripartite mycorrhiza-legume-*Rhizobium* symbiosis is the subject of this review. Mycorrhizal nitrogen-fixing legumes include many important temperate and tropical crops, e.g. clover, lucerne, beans (*Phaseolus* and *Vicia*), peas, soybean, cowpea, pigeonpea, groundnuts, *Stylosanthes*, *Pueraria* and *Centrosema*. These forage and grain legumes form endomycorrhiza of the vesicular-arbuscular (VA) type, as do most species of the Mimosoideae and Papilionoideae. Some arborescent legumes also form VA mycorrhiza, e.g. *Leucaena*, but many, especially the Caesalpinoideae, form mycorrhiza of the ecto-type; some, e.g. *Acacia*, have both ecto- and VA mycorrhiza. In some legumes, e.g. clover and *Stylosanthes*, mycorrhizal fungi can densely colonize >70% of the root system; in others, e.g. lupins, mycorrhizal infection is usually light. Unlike the *Rhizobium* symbiosis, mycorrhizal symbioses are essentially non-specific. The ability of mycorrhizae to increase plant uptake of phosphate and alleviate P-stress in P-deficient soils leads to increases in nodulation, nitrogen-fixation, P concentration and plant growth. Mycorrhizae also affect trace element uptake, e.g. Cu and Zn, photosynthate supply, water relations and hormonal balance in legumes. Some legumes grow so poorly without mycorrhiza as to be ecologically obligately mycorrhizal. To some extent root geometry determines the degree of dependence of a legume on mycorrhiza, because the fungal hyphae extend the absorbing surface of the root. Where a legume is growing with a non-mycotrophic plant, its competitive ability can be increased by mycorrhiza. Environmental factors and inputs of P and N fertilizer affect the effectiveness of the *Rhizobium*-mycorrhiza interaction. Also disease tolerance of legumes can be affected by mycorrhiza. The practical impact of mycorrhiza in nitrogen-fixing legumes may be considerable. Dual inoculation of leguminous crops with elite strains of mycorrhizal fungi and *Rhizobium* bacteria, in conjunction with minimal N fertilizer and better utilization of less P fertilizer (rock or super), is currently being studied in many countries. Inoculation techniques are being developed for exploitation on a field scale. It is hoped that further investigations, especially in low-input cropping systems, will enable the substantial potential of mycorrhiza in legume productivity to be achieved.

## Résumé

*Les mycorhizes des légumineuses fixatrices de l'azote*

La plupart des plantes forment des mycorhizes, c'est à dire des associations symbiotiques des racines avec des champignons. Beaucoup de plantes peuvent aussi former des symbioses avec des bactéries spécifiques ou des actinomycètes qui produisent des nodules racinaires et fixent l'azote atmosphérique dans ces nodules. La symbiose tripartite mycorhize-légumineuse-*Rhizobium* est le sujet de la présente revue générale. Les légumineuses à mycorhizes fixant l'azote comprennent un grand nombre de cultures importantes des pays tempérés et tropicaux, comme le trèfle, la luzerne, les haricots (*Phaseolus* et *Vicia*), les pois, le soja, le cajou, l'arachide, *Vigna sinensis*, *Stylosanthes*, *Pueraria* et *Centrosema*. Ces légumineuses à fourrage et à graines forment des endo-mycorhizes de type vésiculaire-arbusculaire (VA), comme le font le plupart des éspèces de Mimosoideae et de Papilionoideae. Certaines légumineuses arborescentes forment aussi de mycorhizes VA, par exemple *Leucaena*, mais beaucoup d'entre elles, particulièrement les Caesalpinoideae, forment des ecto-mycorhizes. Certaines, comme les *Acacia*, ont à la fois des mycorhizes du type VA et du type ecto. Les champignons mycorhizogènes peuvent densement coloniser (plus de 70%) les systèmes racinaires de

quelques légumineuses comme le trèfle et le *Stylosanthes*, mais ordinairement légèrement colonisent d'autres, eg. *Lupinus*. A la différence des symbioses à *Rhizobium*, celles des mycorhizes sont essentiellement non-spécifiques. L'aptitude des mycorhizes à accroître l'absorption des phosphates et à réduire la déficience en P dans les sols qui en sont pauvres a pour conséquence d'accroître la nodulation, la fixation de l'azote, ainsi que la teneur en P et la croissance de la plante. Les mycorhizes influence également l'absorption des oligo-éléments, comme Cu et Zn, l'activité photo-synthétique, les relations avec l'eau, et l'équilibre hormonal des légumineuses. Certaines légumineuses poussent si mal en l'absence de mycorhizes qu'on peut les considérer, du point de vue écologique, comme obligatoirement mycotrophiques. La géométrie des racines détermine dans une certaine mesure le degré de dépendance d'une légumineuse par rapport au mycorhizes. En effet, les hyphes fongiques accroissent la surface absorbante de la racine. Lorsque une légumineuse pousse avec une plante non-mycotrophique, sa compétitivité peut être accrue par la mycorhization. Certains facteurs de l'environnement, ainsi que l'apport de P et de N par des engrais diminuent l'efficacité de l'interaction *Rhizobium*-micorhize. D'autre part la résistance des légumineuses aux maladies peut être affectée par les mycorhizes. L'impact pratique des mycorhizes sur les légumineuses fixant l'azote peut être considérable. La double inoculation avec des souches sélectionnées de champignons mycorhiziens et de *Rhizobium* bactériens, associée à un apport minimal d'engrais azoté et à une meilleure utilisation d'un moins quantité d'engrais phosophoré (de roche ou super-phosphate), est couramment étudiée dans de nombreux pays. Des techniques d'inoculation sur le terrain sont mises au point. On espère que de nouvelles recherches, en particulier sur les systèmes de culture avec faible apport exogène, permettront au potentiel des mycorhizes pour la productivité des légumineuses de se réaliser pleinement.

## Resumen

### Micorrizas de leguminosas fijadoras de nitrógeno

La mayoría de las especies vegetales forman micorrizas, que son asociaciones simbióticas hongo-raíz. Muchas plantas pueden también formar simbiosis con bacterias específicas o actinomicetos, produciendo nódulos radicales fijadores de nitrógeno atmosférico. La simbiosis tripartita micorriza-leguminosa-*Rhizobium* constituye el tema de esta revisión. Entre las leguminosas micorrizables y fijadoras de nitrógeno se incluyen cultivos importantes tanto de climas templados como tropicales, como son trébol, alfalfa, judía (*Phaseolus* y *Vicia*), guisante, soja, freijol, guandú, cacahuete, *Stylosanthes*, *Pueraria* y *Centrosema*. Estas leguminosas forrajeras o de grano forman endomicorrizas del tipo vesículo-arbuscular (VA), al igual que la mayoría de las especies de las Mimosoideae y Papilionoideae. Algunas leguminosas arborescentes como *Leucaena* también forman micorrizas VA aunque la mayoría, especialmente las pertenecientes a las Cesalpinoideae forman micorrizas de tipo ecto-, aunque se han citado casos como en *Acacia* que poseen ambos tipos de micorrizas, ecto y VA, simultaneamente. En algunas leguminosas (trébol y *Stylosanthes*) el hongo micorrícico puede colonizar densamente (más del 70%) el sistema radical; en otros casos (*Lupinus*) la infección micorrícica es por lo general leve. Al contrario de lo que ocurre con *Rhizobium*, las simbiosis micorrícicas son esencialmente no específicas. La capacidad de las micorrizas para incrementar la absorción de P por la planta, superando así la deficiencia en fosfato de los suelos pobres en P, conduce a un incremento de la nodulación, fijación de nitrógeno, concentración de P y crecimiento de la planta. Las micorrizas también afectan la absorción de oligoelementos como Cu y Zn, la distribución de fotosintato, las relaciones hídricas y el balance hormonal en las leguminosas. Algunas leguminosas crecen con tan poco vigor en ausencia de micorrizas que pueden considerarse, desde un punto de vista ecológico, como obligatoriamente micorrícicas. Hasta cierto punto, la geometría de la raíz determina el grado de dependencia de una leguminosa de la micorriza, ya que las hifas del hongo aumentan la superficie absorbente de la raíz. Cuando una leguminosa crece junto con una planta no micorrizable, su capacidad competitiva puede incrementarse gracias a la micorriza. Diversos factores ambientales y el aporte de fertilizantes de N y P afectan la eficacia de la interacción *Rhizobium*-micorriza. La tolerancia de las leguminosas a distintas enfermedades puede verse también afectada por las micorrizas. El impacto práctico de las micorrizas en las leguminosas fijadoras de nitrógeno puede ser considerable. En muchos países se está estudiando el efecto de una doble inoculación de

cultivos con cepas seleccionadas de hongos micorrícicos y de *Rhizobium* junto con un aporte mínimo de nitrógeno y una mejor utilización de menor cantidad de abono fosfatado (de roca o superfosfato). Se están desarrollando distintas técnicas de inoculación para su explotación a nivel de campo. Se espera que el resultado de estas y otras investigaciones, especialmente en el área de sistemas agrícolas de bajo consumo, permita a las micorrizas desarrollar plenamente su papel en la productividad de las leguminosas.