Mycorrhiza in tropical agriculture

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SUMMARY

The paper highlights the important role vesicular-arbuscular (VA) mycorrhiza can play in the improvement of tropical agriculture. The biology of mycorrhiza and the effect of the fungus on plant growth and P uptake have been briefly reviewed. The effect of VA mycorrhiza in improving the efficiency of commercial phosphorus fertilizers has also been emphasized and suggestions for possible use of the fungi to aid the production of field crops in tropical agriculture have been made.

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RÉSUMÉ

OWUSU-BENNOAH, E.. *La mycorrhiza dans l'agronomie tropicale.* Ce rapport souligne l'importance de la mycorrhiza vasiculaire-arbusculaire (VA) dans l'agronomie tropicale. La biologie de la mycorrhiza et l'effet de fongi sur la croissance de plante et l'utilisation de P ont été décrit concisement. L'effet de la mycorrhiza VA dans l'amélioration de l'efficacité d'engrais a base du phosphore a aussi été souligné et des conseilles donné à ce que concerne l'utilisation possible de fongi pour aider la production des cultures dans des millieux tropicales.

Introduction

One major problem facing tropical agriculture is the low fertility status of the soils. Very few tropical soils contain sufficient nutrients, notably nitrogen and phosphorus in forms suitable for sustaining good crop yields. Therefore, large dressings of P-containing fertilizers are often needed to satisfy the phosphate adsorption sites of the soils and to raise the equilibrium phosphate concentration in the soil solution to a level adequate (usually between 0.01 - 0.4 ppm) for maximum plant growth. Even on the more productive tropical soils, regular applications of P-fertilizers are necessary. Nevertheless, not only are fertilizer applications in general expensive to the majority of peasant farmers but also P-fertilizers in particular are extremely inefficient. For example, about 75 per cent of P-fertilizer input is reverted to unavailable phosphorus forms which plants cannot tap.

It therefore becomes necessary to look at ways and means of economizing on P-fertilizer usage, while still maintaining high yields of tropical crops. One possible way stems from observations over a century that many crop plants can have substantially better growth when their root system are infected with symbiotic fungi, and are as such mycorrhizal. These observations have interested farmers and scientists who view the phenomenon as a means of increasing agricultural production. Unfortunately, tropical agriculture has not benefited greatly from vesicular-arbuscular mycorrhizal research mainly because very little is so far known about mycorrhizal relations in many tropical plants. The objective of the paper therefore is to review the biology of the symbiosis with reference to the role which mycorrhiza can play in the improvement of arable crop yields in the tropics.

Definition of mycorrhiza

Mycorrhiza, a Greek word meaning fungus-root, is defined as a mutualistic symbiosis between the roots of higher plants and certain fungi (Harley, 1969). Basically, mycorrhiza are of two types, namely ectomycorrhiza and endomycorrhiza. In the ectomycorrhiza association, the fungus forms a thick sheath of mycelium around the feeder roots of the host plants;

it also penetrates between the cells of the root cortex but not generally within them. On the other hand, in endomycorrhiza, the fungal partner grows mainly inside the root cortex and intracellular penetration is normally the mode of entry. The lack of external sheaths in endomycorrhiza association makes it difficult to recognize the fungus without special techniques, usually involving staining and microscopic examination (Phillips & Hayman, 1970).

In natural ecosystems, it is exceptional for a plant not to possess a mycorrhizal root system. Ectomycorrhiza-forming species are mostly forest trees, such as pines and eucalyptus. Endomycorrhizae, in contrast, are formed in all climates by most herbaceous species, including the majority of agricultural crops, most tropical and some temperate tree species. According to Gerdemann (1986), only a few plant species, for example, Cruciferae and Chenopodiaceae, appear to contain any number of non-mycorrhizal species.

The commonest and the most widespread of the endomycorrhiza is the vesicular-arbuscular type. The fungal symbionts in VA mycorrhiza belong to the family Endogonaceae with four genera, notably the *Glomus, Acaulospora, Gigaspora* and *Sclerocystis* (Gerdemann & Trappe, 1974). All attempts so far to grow VA mycorrhiza in axenic culture in the absence of a host plant have failed. The only way of producing them at the moment is by infecting a host plant with the fungi. Unlike other obligate associations, there is very little evidence of specificity, as any single VA fungi isolate can apparently form mycorrhiza with an extremely wide range of host species (Mosse, 1975).

The VA fungi form the largest resting spores known, and have sometimes in the past been mistaken for nematode microcysts. After forming an appressorium on the root surface, the penetration hypha ramifies in the root cortex. Branches from the longitudinally running intercellular hyphae enter cells where further branching results in historical structures termed arbuscules. Hyphal swellings, termed vesicles, form on the mycelium inside and outside the root as the infection ages.

TABLE 1

Published Field Experiments on Inoculation with VA Mycorrhiza

Crop	*VA species*	*Growth Increase*	*Country*	*Reference*
Maize	*G. mosseae*	×3	Nigeria	Islam (1977)
Cassava	*G. mosseae*	×3	Nigeria	Islam (1977)
Cassava	*G. mosseae*	×3	Nigeria	Ayanaba & Sanders (1981)
Water yam	*G. mosseae*	×4	Nigeria	Ayanaba & Sanders (1981)
Yam	*G. mosseae*	×3	Hawaii	Vander Zaag *et al.* (1979)
Cocoa	*G. gigantea*	×3	Trinidad	Laycock (1945)
Oil palm	*G. gigantea*	×2	Malaysia	Nadarajah (1980)
Rubber	*G. acaulospora*	×2	Malaysia	Waidyanatha (1980)
Cowpea	*G. mosseae*	×2	Nigeria	Islam (1977)

Effect of VA mycorrhiza on plant growth

There has been improved growth in many tropical agricultural plants resulting from improved P-nutrition due to their roots being mycorrhizal. Table 1 gives some examples of published field experiments in some tropical countries. Although the presence of VA mycorrhiza can increase several fold, the efficiency with which a plant root extracts P (Table 2) (Owusu-Bennoah & Mosse, 1979; Owusu-Bennoah & Wild, 1979; Pichot & Truong, 1980), mycorrhizal roots do not have access to forms of soil P unavailable to non-mycorrhizal roots as shown in Table 3 (Sanders & Tinker, 1971; Owusu-Bennoah & Wild, 1980).

Instead, the external mycelium is able to absorb and translocate into the root phosphorus from a volume of soil much larger than that exploited by non-mycorrhizal roots. This is critical because, unlike other major nutrients, uptake of phosphate is limited by the very low diffusion coefficient of the phosphate ion in soil (Tinker, 1975). According to Nye (1966) and Baylis (1970), root hairs act in an analogous manner but usually less efficiently. Thus in tropical soils where P supply limits plant growth, mycorrhizal infection can result in growth response, and the greater the proportion of the root system that is mycorrhizal, the greater the response.

TABLE 2

Phosphorus Content of Mycorrhizal and Non-mycorrhizal Onions Grown in Seven Soils

Soil no.	Total P/plant (mg)			
	Mycorrhizal plants		Non-mycorrhizal plants	
	Shoots	Roots	Shoots	Roots
7	0.64	0.49	0.02	0.02
8	0.16	0.17	0.13	0.13
10	0.12	0.09	0.05	0.05
11	0.82	0.51	0.08	0.05
12	0.65	0.57	0.26	0.22
15	0.07	0.07	0.04	0.04
16	0.68	0.61	0.51	0.52

Mean of six plants (Hayman & Mosse, 1972)

TABLE 3

Specific Activities of Phosphorus Absorbed by Mycorrhizal and Non-mycorrhizal Onion Grown in Seven Soils

Soil no.	cpm/µg P taken up			
	Mycorrhizal plants		Non-mycorrhizal plants	
	Shoots	Roots	Shoots	Roots
7	4.6	4.4	4.5	3.7
8	11.1	9.7	10.2	10.1
10	18.1	24.7	23.1	20.4
11	2.2	2.1	2.0	1.9
12	1.9	2.1	2.1	2.0
15	28.0	26.1	25.6	23.8
16	2.0	1.9	1.7	1.9

Mean of three replicates (Hayman & Mosse, 1972)

Table 4 indicates that although mycorrhizae do not directly increase breakdown of phosphate rock, they can improve recovery of P from such low grade sources, especially in acid soils (Mosse, 1977). The hyphae or mycorrhizal fungi can come into closer contact than roots with particles of the fertilizer and efficiently absorb phosphate ions as they become chemically dissociated by the acid conditions (Murdoch, Jackobs & Gerdemann, 1967; Cabala-Rosand & Wild, 1982).

The importance of this is that mycorrhizal plants extract phosphorus from the soil much more efficiently, reducing fertilizer requirements. Their ability to cope with less soluble phosphate would be of an advantage for poor countries which have rock phosphate deposits or cannot afford the more

TABLE 4

Response of Stylosanthes guyanensis *to Mycorrhizal Inoculation and Rock Phosphate in Three Unsterile Soils from Three Countries (Mosse, 1977)*

Treatment	Nil	RP	M	M + RP
Soil no. 7; Egbeda IITA, Nigeria (8 weeks from transplanting 1 plant /pot)				
Dry weight (g)	0.37	0.42	0.78	0.87
Total P (mg)	0.62	0.70	1.08	0.93
Nodule number	43	51	79	78
N_2 fixation	0.57	0.86	0.85	0.48
Infection %	20*	80*	50*	35*
Soil no.9; Brazil (9 weeks from transplanting 1 plant/pot)				
Dry weight (g)	0.55	0.93	0.51	1.23
Total P (mg)	0.76	1.83	0.63	2.18
Dry weight nodules (mg)	7	15	6	20
N_2 fixation	1.15	1.86	0.79	3.31
Infection %	70*	25*	65*	65*
Soil no. 10; Bambey Senegal (9 weeks after transplanting 2 plants/ pot)				
Dry weight (g)	0.31	0.28	0.34	0.88
Total P (mg)	0.48	0.64	0.47	2.05
Nodule dry weight (mg)	5	4	4	15
N_2 fixation	0.92	0.71	0.65	0.95
Infection %	50*	80*	50-80*	25*

RP = rock phoshate, M = inoculated with endophyte E_3

* Indigenous and introduced endophyte.

expensive and soluble sources. Various studies have shown that phosphate is absorbed by the external mycelium of the fungus and translocated into the host root partly as polyphosphate (Cox, Sanders, Tinker & Wild, 1975). It is then released into the host probably *via* the arbuscules, although there is still controversy as to the exact mechanism involved (Tinker, 1975).

Effect of mycorrhiza on water uptake

Water relations of mycorrhiza have been little studied but this may be particularly important in sandy soils and in the semi-arid tropics. Available evidence seems to suggest that water supply from soil could be improved by VA mycorrhiza (Safir, Boyer & Gerdemann, 1971; Sieverding, 1979). Theodorou (1978) has also shown that some ectomycorrhizal fungi can grow at much lower water potential than higher plants and thus make a significant contribution to water uptake by the root in some soils. Two mechanisms of mycorrhizae mediated water effects have been advanced: (i) Improved P nutrition (ii) Hormonal control (Safir, Boyer & Gerdemann, 1972; Levy & Kirkun, 1980).

Interaction with other soil micro-organisms

It has been observed in most tropical soils that several legumes nodulate very poorly unless they are inoculated with *Rhizobium* spp. This has been attributed to phosphorus deficiency because, according to Schreven (1958), an adequate phosphorus supply is necessary for satisfactory nodulation and nitrogen fixation. Synergism between VA mycorrhizae and nitrogen-fixing bacteria (*Rhizobium* spp.) has now been established in legumes (Mosse, 1977; Halos, Luvis & Borja, 1982); mycorrhiza inoculation has led to better nodulation with *Rhizobium* spp. and increased nitrogen fixation in pot and field experiments (Crush, 1974; Young, Juang & Chao, 1988). Using VA mycorrhiza and *Rhizobium* spp. as a combined inoculant, Ross (1971) and Halos & Borja (1980) found that *Glomus mosseae* largely facilitated nodulation, nitrogen fixation and growth in some legumes such as soybean, cowpea, clover and French beans.

According to Waidyanatha, Yogaratman & Ariyathe (1978), mycorrhizal infection may be more important for nitrogen fixation in legumes than for plant growth *per se*. This is due to the greater requirement of phosphate for nodule activity than for plant growth.

Some beneficial soil micro-organisms, such as the phosphate-solubilizing bacteria, may also act synergistically with mycorrhizal fungi (Barea, Azcon & Hayman, 1975). Azcon, Barea & Hayman (1976) suggested that both the phosphate-solubilizing bacteria and VA mycorrhiza could use phosphorus more effectively in the form of insoluble rock phosphate added to soil than in the insoluble forms of phosphate that occur naturally in soils. Inoculation of *Endogone* (E3) with *Cylindrocarpon destructans* caused a significant increase in dry matter weight of *Fragaria* seedlings. This was attributed to the synergism between the VA mycorrhiza and the fungus (Paget, 1975).

VA mycorrhizae have also been demonstrated to have a marked effect on other micro-organisms in the rhizosphere, including many plant pathogens. For example, Ross (1972) found that an endomycorrhizal fungi, *Endogone* sp., increased the susceptibility of soybean to *Phytophthora megasperma*, while Baltruschat, Sikora & Schonbeck (1973) indicated *Endogone mosseae* had an antagonistic effect on *Thielavia basicola*, and also *Meloidogyne incognita* on tobacco. Suppressive effects of some VA mycorrhizae on root-knot nematodes on soybeans have also been shown clearly by Schenck, Kinlock & Dickson (1975). Parvathi, Venkateswarlu & Rao (1985) reported that root-infecting fungi such as *Fusarium solani* or *Rhizoctonia solani* do not exert any antagonistic effects on the mycorrhizal endophyte, *Glomus mosseae*, once they colonized and established in roots.

Can mycorrhizae be used to improve efficiency of fertilizer in tropical agriculture?

The utilization coefficient of P in commercial fertilizers does not exceed 10 per cent and can be as low as 1 per cent under certain conditions in the tropics. This means that about 90 per cent of fertilizer is immobilized in the soil (Fardeau, 1984). Considering the increased costs of chemical fertilizers, especially in developing countries, there is the need to now consider possible ways in which VA mycorrhizal fungi can be used to aid the production of tropical crops. Mycorrhizae cannot totally replace fertilizers but they could permit a better exploitation of phosphate reserves in soils, a higher efficiency of fertilizer recovery and therefore more rational use of applied fertilizer (Gianinazzi-Pearson, 1986).

Non-mycorrhizal plants growing in low to moderately fertile soils frequently require a supply of soluble phosphate in order to improve their phosphate nutrition and productivity to a level similar to that of mycorrhizal plants growing without addition of fertilizer (Tinker, 1975; Gianinazzi-Pearson, 1986). Mycorrhizae can indeed be used to economize and even partially substitute for phosphate fertilizer. The same is true for highly phosphate fixing soils in the tropics where most of the available phosphate added as fertilizer becomes rapidly immobilized. Mycorrhizae increase the phosphate-recovering power of plants in such soils; they rapidly deplete the soil solution P so that phosphate is drawn into solution from the adsorbed or fixed fraction of the labile pool phosphate (Tinker, 1975; Owusu-Bennoah & Wild, 1979).

There are many situations where plants are produced in sterilized field of nursery soils, or in potting mixtures devoid of mycorrhizal fungi. Growers compensate for the absence of mycorrhizae by supplying luxury amounts of fertilizer. Many crops produced in this way, such as citrus fruits, are mycorrhizae-deficient; the introduction of mycorrhizal inoculation into the production programme could thus allow substantial reductions in fertilizer rates without reducing the marketable quality of the crop (Johnson & Menge, 1982). In certain cases, like citrus, introduction of mycorrhizal fungi into fumigated nursery soils is not only recommended but is considered essential for maximum growth (Menge, Labanauskas, Johnson & Platt, 1978).

Suggestions for future research

For tropical crops to benefit from VA mycorrhiza, there is the need to know the most mycotrophic plants which derive most benefit from mycorrhizal root infections. Available evidence seems to indicate that generally plants with a high P demand and poor root system, unable to explore much soil volume, are the most likely to respond to mycorrhizal formation (Baylis, 1970).

Where agricultural biocides have adverse effects on the mycorrhizal fungi, increased disease and pest control may not always outweigh the loss of mycorrhizal benefits in terms of nutrient uptake (de Bertóldi, Giovannetti, Griselli & Rambelti, 1977). Such side effects, therefore, need to be carefully studied.

To derive maximum benefit from VA mycorrhiza, it is necessary that high populations of the fungus be maintained. Mycorrhizal population can be influenced by cultural practices, such as fertilizer application and crop rotations (Hayman, 1975; Kruckelmann, 1975). Where infection by indigenous VA fungi has a marked effect on growth, previous cropping may influence the subsequent crop in terms of mycorrhizal infection, apart from residual nutrient effect and disease carryover. Modifications of cropping sequence and cultivation techniques may prove necessary if high populations of VA fungi are to be maintained.

Accumulating evidence indicates that species of VA mycorrhizae differ greatly in their ability to aid host P uptake in some soils (Mosse, 1973). It is probable that many tropical soils carry populations of VA fungi that survive in the particular environment but are not intrinsically very effective in combination with a particular host crop. Furthermore, species differences in tolerance of fertilizer (Hayman, 1975) suggest another means of manipulating existing soil populations or introducing new species.

If populations of VA fungi are successfully manipulated in tropical soils so as to maintain large populations of species or strains well suited to the particular host crops, it may prove possible to allow a run-down of P in many soils without loss of yield. In the case of improvement of acid soils, lower initial inputs of fertilizer-acid result from an introduction of appropriate species of VA fungi. At present, it is impractical to produce mycorrhizal inoculum on a sufficient scale for large field applications because the fungi have to be reproduced in pots containing stock plants. Pure cultures of the fungi, unlike *Rhizobium* inoculum, are unavailable. Nevertheless, inoculation is clearly worth pursuing, and production of a pure culture of the fungi must engage the attention of both mycorrhizaists and non-mycorrhizaists.

Conclusion

It must be emphasized that the potential of VA mycorrhiza in improving tropical agriculture, especially in cutting down chemical fertilizer consumption, is great. The roots of most tropical plants in the wild have this association with fungi, but the manipulation of the natural environment to obtain more production out of plants has upset the relationship in cultivated plants. There is a great deal of evidence that soil fumigation to destroy certain target pathogens, weeds and insects before planting also kills the fungi. The stunting of many nursery crops, where soil fumigation is extensively used, has been traced to the destruction of mycorrhizal fungi. The great potential of VA mycorrhizae should therefore be harnessed on a field scale to the benefit of tropical agriculture.

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