MYCORRHIZAE AS A MAJOR FACTOR OF SOIL FERTILITY

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SUMMARY

In this general presentation on mycorrhizae, particular emphasis is placed on knowledge concerning those aspects most relevant to practical applications of these synmbioses in plant production. After a brief introduction, the influence of mycorrhizae on the mineral nutrition of plants is outlined and the edaphic conditions, biological factors and management practices affecting mycorrhiza development and function are described. Mycorrhiza biotechnology is as yet little developed, research in this field is very recent and major obstacles still have to be overcome. The potential of mycorrhizae for the production of nursery plants in disinfected soils or soil-less rooting media is discussed, together with the problems limiting their use for large-scale crop production in nondisinfected field soils.

INTRODUCTION

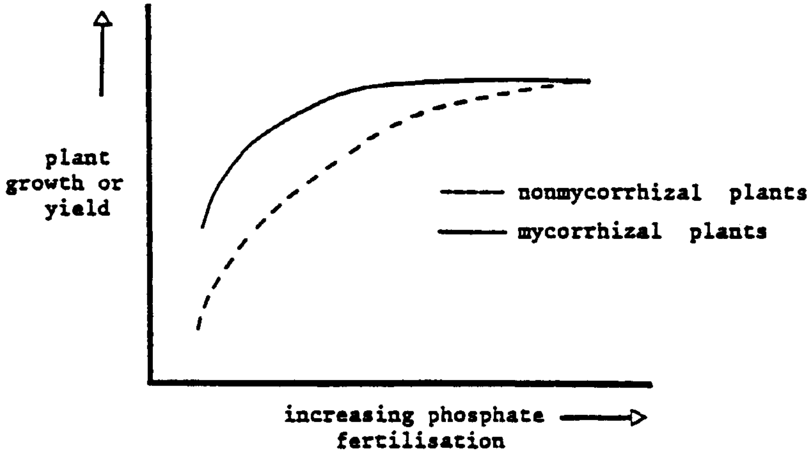
Mycorrhizae are the most widespread root symbioses occurring in nature and they represent an important contributing factor to soil fertility which is frequently ignored or underestimated. It is not very difficult to demonstrate the impact that mycorrhizae can have on crop production, especially in soils with a low nutrient status. Soil disinfection often leads to retarded plant growth, reflecting a decrease in soil fertility which can only be overcome by introducing mycorrhizal fungi into the soil (GIANINAZZI et al., 1982 ; HARLEY and SMITH, 1983 ; GIANINAZZI-PEARSON, 1986).

Briefly, mycorrhizae are formed by nearly all plants and there are two main types which are economically and ecologically important both in temperate and tropical climates (GIANINAZZI-PEARSON and DIEM, 1982 ; REDHEAD, 1982 ; GIANINAZZI-PEARSON, 1984). About 3 to 5 % of species in the plant kingdom, most of which are forest dominant woody angiosperms or gymnosperms, form ectomycorrhizae. Here the fungi, principally basidiomycetes and ascomycetes, develop a fungal sheath on the root surface and a Hartig net of hyphae between epidermal and cortical cells. More than 80 % of plant species, however, form vesicular-arbuscular (VA) endomycorrhiza ; this type of mycorrhiza concerns the large majority of agricultural and horticultural crops, as well as fruit and forest (especially tropical) trees. In this type of mycorrhiza, the fungal symbiont, a zygomycete, develops normally within the root tissues where it forms characteristic vesicles and intracellular haustoria (arbuscules).

Mycorrhizal effects on plant growth

There are several ways in which these symbiotic associations can affect plant physiology and lead to better plant growth, but their major rôle is to improve plant mineral nutrition and consequently soil fertility (see GIANINAZZI et al., 1982 ; GIANINAZZI-PEARSON and GIANINAZZI, 1986). Both VA endomycorrhiza and ectomycorrhiza can improve the absorption by roots of such poorly mobile ions as phosphate, ammonium and certain trace elements. This effect is mainly explained by the fact that the network of hyphae developing out from mycorrhizal roots can absorb these nutrients, transport them to the root and release them to the host cells. In this way, the fungi provide the plant with an important diffuse absorbing surface in the soil, so enabling absorption of mineral nutrients from the soil solution beyond the depletion zone, which for poorly mobile ions rapidly develops at the root surface and impedes direct absorption by the root cells.

Most is known about the phosphate nutrition of mycorrhizal plants. Mycorrhizal growth responses are greatest in phosphate-poor soils or in soils with a high phosphate-fixing capacity (e.g. clay soils, andosols, oxisols,...). If supplies of soluble posphate to a soil are increased, the effect of mycorrhizae on plant growth decreases. This is because the nonmycorrhizal plants respond more than the mycorrhizal plants to fertilizer applications, as illustrated in the following typical response curves :



Where the two curves meet will depend on the plant, the mycorrhizal fungus and the soil involved. Researchers often use values for soluble phosphate obtained by Olsen's extraction method to predict mycorrhizal reponses, but the best indicator seems to be the actual quantity of phosphorus in the soil solution (YOST and FOX, 1979, MENGE et al. 1982 ; OJALA et al., 1983).

Mycorrhizal plants absorb phosphate from the same fraction of soil phosphorus as nonmycorrhizal plants, that is principally from the available pool of phosphorus. Mycorrhizae do not have any special direct effect on insoluble phosphates and they cannot improve the direct utilisation of poorly soluble fertilizers like rock phosphate (GIANINAZZI-PEARSON et al., 1981 ; AZCON G. DE AGUILAR et al., 1986). They can, however, have indirect effects, especially in acid soils where they will rapidly and efficiently absorb phosphate ions released from such fertilizers by the soil acidity (CABALA-ROSAND and WILD, 1982).

Factors affecting mycorrhiza development and function

As for other symbioses, like nitrogen fixing associations, the potential of mycorrhizae to improve soil fertility and plant production depends very much on environmental and biological factors (MOSSE et al., 1981 ; GIANINAZZI-PEARSON and DIEM, 1982 ; GIANINAZZI-PEARSON, 1984).

Soil factors affecting mycorrhizal infection development and mycorrhizal effects are principally the pH and mineral nutrient availability, especially phosphate. Mycorrhizal fungi often show adaptation to pH, and species or isolates can have quite different pH requirements. For certain fungi, heavy fertilization can lead to reduced infection whilst others show a marked tolerance, for example, to high levels of plant-available phosphate in soils. Furthermore, species or isolates of mycorrhizal fungi can also vary in their tolerance to extreme temperatures or water stress conditions.

Mycorrhizal fungi not only differ in their edaphic requirements but also in their ability to stimulate growth of host plants. In fact, although ectomycorrhizal and VA mycorrhizal fungi are not host specific, the efficiency of a mycorrhizal system will partly depend on the physiological characteristics of the fungal symbiont (ability to translocate and transfer nutrients), the amount and distribution of the soil mycelium and, as already mentioned, on interactions between the fungal species or isolates and the environment. This varability opens the possibility of selecting efficient fungi that are well-adapted to specific edaphic conditions, in order to ensure their success when introduced into a given ecosystem.

Host genotype is also determinant for the development and effectiveness of mycorrhizal associations, and mycorrhizal dependency, the degree to which a plant relies upon the mycorrhizal condition for maximum growth or yield at a given level of soil fertility, can vary greatly between plant species and even cultivars. In general, plants having coarse roots and few root hairs like tree species, woody plants and liliaceous plants are highly mycorrhiza dependent whilst herbaceous legumes are less, and cereals which have fine roots with long, dense root hairs generally show little or no mycorrhizal dependence under field conditions of moderate fertility.

A certain number of agricultural management practices can affect mycorrhiza development and function. Heavy fertilization, as previously mentioned, and the use of pesticides, especially biocides and fungicides (TRAPPE et al., 1984), can greatly reduce fungal populations and mycorrhizal infection levels. Others like soil disinfection, micropropagation techniques or the use of soil-less rooting media, completely eliminate mycorrhizal fungi and can cause stunting or transplantation problems for mycorrhiza-dependent plant species (LETACON and GIANINAZZI-PEARSON, in press). In fact, mycorrhiza biotechnology is presently being used to ensure the production of certain nursery crops like forest trees (see CHIPOMPHA, this volume), citrus (MENGE, 1984) and bell-pepper (HASS et al., 1986) grown in soils that have been disinfected to eliminate pathogens or weeds.

Inoculation and mycorrhizal inoculum

Although inoculation of mycorrhizal fungi can be beneficial for highly mycorrhiza-dependent plants growing in disinfected soils, most soils are not disinfected. Because of the widespread occurrence of mycorrhizal fungi (MOSSE et al., 1981), it is therefore essential to first characterize indigenous populations in order to know whether inoculation of selected fungal symbionts will be worthwhile or not. There is little point in inoculating if indigenous mycorrhizal fungi are abundant and highly effective but it is interesting to ensure that their populations are maintained and to avoid management practices that could reduce them. Ineffective populations of indigenous mycorrhizal fungi can, however, occur in soils (DODD et al., 1983 ; BLAL, 1985 ; GIANINAZZI-PEARSON et al., 1985) and inoculation of more effective fungi can improve plant growth in nondisinfected soils (see for example : ABBOTT and ROBSON, 1978 ; AZCON-AGUILAR and BAREA, 1981 ; KUO and HANG, 1982 ; POWELL, 1984).

There is no doubt that mycorrhizae are an important factor of soil fertility but their application in plant production still remains limited mainly due to the fact that mycorrhiza inoculum for the large majority of plants is not yet produced on a real commercial scale. Many fungi forming ectomycorrhiza can be grown in pure culture, inoculum can be produced on solid or liquid media and viable commercial inoculum for a certain number of fungi is now available both in the USA and in France (LETACON and GIANINAZZI-PEARSON, in press). VA mycorrhizal fungi, on the contrary, cannot be cultured on synthetic media and the fungi have to be maintained on roots of living host plants growing in sterile soil or rooting media under nonsterile conditions. Inoculum produced in this way can consist of infested soil, mycorrhizal roots and/or spores. Inoculum pellets of mycorrhizal roots and/or spores have been manufactured with or without seeds using soil, methyl cellulose, $CaCO_3$ or calcium alginate as binding agents (HALL and KELSEN, 1981 ; HAYMAN et al., 1981 ; GANRY et al., 1982). However, VA mycorrhizal inoculum can currently only be produced economically and in large enough quantities on living host plants under greenhouse conditions. Crude inoculum (soil, roots, spores) produced in this way can be of good quality and has been used successfully in nurseries and in field trials around the world.

An impossibility to produce pure inoculum does not necessarily exclude the use of mycorrhizae to improve soil fertility. With a better knowledge of indigenous populations in different soils and sites, for example, advantage may be taken of efficient ones to eventually inoculate nursery plants *in situ* before their transplantation into mycorrhiza-poor sites.

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