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# MYCORRHIZAE IN SOYBEAN DEVELOPMENT, NUTRITION AND STRESS PHYSIOLOGY

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## ABSTRACT

Mycorrhiza formation has fundamental effects on the development, nutrition and physiology of the soybean plant. The most obvious, and best-known, of these is the improvement in phosphorus nutrition. Other effects are changes in the relative development of roots, shoots, leaves and nodules, in the allocation of nutrients to plant organs and to the bacterial and fungal endophytes, in the physiology of symbiotic functions such as photosynthesis and nitrogen fixation, and in the host's response to environmental and biological stress. In general, the mycorrhizal symbiosis is mutualistic, benefiting both host and endophyte.

## INTRODUCTION

A mycorrhiza (fungus root) is a symbiotic association between a plant root and a soil fungus. The organisms of interest in agricultural applications are known as vesicular-arbuscular mycorrhizal (VAM) fungi. Soil mycelia of VAM fungi are organs of nutrient exchange in the soil, while the root mycelium facilitates this transfer within the cells of the root cortex. Thus, VAM fungi are a major factor in plant-soil interactions. Establishment of the mycorrhizal association has a profound effect on the host plant. The best known result is an improvement in host-plant P nutrition when soil P is limiting; this is often thought of as 'the mycorrhiza effect'. In fact, many aspects of the host's ontogeny are affected, such as nutrient acquisition and allocation, morphology, seed yield and composition, physiological functions, including photosynthesis and nitrogen fixation, and resistance to environmental and biological stress.

Although much of the research on mycorrhizae does not use soybeans (*Glycine max* (L.) Merr.) as its experimental vehicle, insights from nonsoybean work are applicable to soybeans also. Sources of general reference (Barea and Azcon-Aguilar 1983, Gianinazzi-Pearson and Gianinazzi 1986, Powell and Bagyaraj 1984, Safir 1987, Smith and Gianinazzi-Pearson 1988, and the compendia of the North American Conferences on Mycorrhizae) are therefore equally relevant to soybeans. What follows here will be restricted mainly to what is known about VAM effects on soybeans and represents a database which has not yet been assimilated by the soybean review literature (Wilcox 1987).

## MEASUREMENT

An assessment of the extent of root and soil colonization by VAM fungi (Schenck 1982) is essential to establish their effect on host plant and host soil. Rapid histological methods not requiring specialized equipment have been developed to estimate the extent of root colonization (Giovanetti and Mosse 1980) and may be supplemented by quantitative measurements (Bethlenfalvay *et al.* 1981). The soil mycelium is more difficult to assess for quantity (Bethlenfalvay and Ames 1987) and activity (Sylvia 1988). VAM fungi cannot be propagated in host-free culture. The soil inocula commonly used contain unknown and highly variable numbers of viable propagules. An evaluation of the inoculum potentials of different fungal isolates is of consequence for purposes of comparison and has been recently reviewed (Franson and Bethlenfalvay in press).

## HOST AND ENDOPHYTE DEVELOPMENT

Development of a mycorrhiza starts with a successful encounter by a root and a germinating spore or other VAM-fungal propagule. The factors which influence its establishment are not well known, but the interplay between P nutrition and C metabolism of the host is thought to be an important determinant (Siqueira *et al.* 1984). Levels and composition of root exudation, controlled by P-status mediated changes in plasmalemma permeability (Menge *et al.* 1978), may play a role not only in the infection process, but also in the association of VAM-fungal species with different host plants (Schenck and Kinloch 1980).

Plants differ greatly in their mycorrhizal dependence, as measured by increased growth relative to nonVAM plants (Ojala *et al.* 1983), with soybeans ranking medium-to-high on a loosely-defined scale (Mosse 1986). Environmental factors such as temperature (Schenck and Schroder 1974) and light (Bethlenfalvay and Pacovsky 1983) affect the endophyte's development, perhaps mediated by the host's own responses. Under given levels of soil P availability (Bethlenfalvay *et al.* 1983), the endophyte may proliferate greatly. When this occurs, the host's cost/benefit ratio (C lost/P gained) may turn negative, resulting in growth depression (parasitism), a condition which appears to be fully reversible (Bethlenfalvay *et al.* 1982a). In soybean, the development of VAM-fungal biomass parallels that of plant growth during the vegetative phase and that of seed development during the reproductive phase (Bethlenfalvay *et al.* 1982b).

## NUTRITION AND SOURCE-SINK RELATIONS

In a tripartite (mycorrhizal, nodulated) legume association growing in soil limiting in N and P, the symbionts are sources of P, N and C, respectively, and are sinks of the products of their symbiotic partners. The allocation of limiting resources is subject to inter-symbiont competition (Bayne *et al.* 1984). Relief from limitation may produce a synergistic growth response in the tripartite symbiosis (Badr El-Din and Moawad 1988). The most important contribution of VAM fungi to this response is the enhancement of P uptake (Munns and Mosse 1980) mediated by the more pervasive root system and by the more efficient depletion of P from dilute solutions (Karunaratne *et al.* 1986) by VAM plants. The uptake of nutrients other than P is also affected by VAM colonization. Both increases and decreases in micro- and macro-nutrients have been reported, and the changes differ with P availability and endophyte species (Lambert *et al.* 1979, Siqueira and Paula 1986). Significantly, interactions between fertilizer regimes and VAM fungi have been shown to affect not only seed yield, but also nutrient and protein composition (Maddox and Raines 1987).

## NITROGEN FIXATION

An essential condition for nodulation and nodule activity is P sufficiency of the host (Mosse 1976). Since VAM fungi can satisfy this condition, the positive VAM effect on nodule activity, which is always observed when P availability is low (Barea and Azcon-Aguilar 1983), has been ascribed to P nutrition (Carling *et al.* 1978). Stimulation of nitrogenase activity by VAM can occur early in plant development and precede plant growth responses (Asimi *et al.* 1980). This may be due to direct and preferential enhancement of nodule function by VAM fungi, or it may be mediated by changes in host nutrition (Cluett and Boucher 1983). Alternatively, VAM fungi may have an influence on symbiotic functions by stimulating the host to produce secondary metabolites (Morandi *et al.* 1984). Although virtually nothing is known about the direct interaction between the nitrogen-fixing organism and the VAM fungus (Hayman 1986), work with nutritionally equivalent plants indicates the existence of antagonistic as well as mutualistic influences (Bethlenfalvay *et al.* 1985) between the micro-symbionts and the existence of preferential *Rhizobium* strain *vs.* VAM-fungal species combinations (Bayne and Bethlenfalvay 1987). The nitrogen-fixing potential of the soybean association is therefore likely to be conditioned not only by the characteristics of the diazotroph-host plant combination (Dreyfus *et al.* 1988) but also by its compatibility with the native VAM mycoflora of areas where soybeans are introduced.

## PHOTOSYNTHESIS

Rates of photosynthesis have been shown to be higher in VAM than in nonVAM plants (Smith and Gianinazzi-Pearson 1988). In view of the role of $P_i$ in regulating $CO_2$ fixation and that of VAM fungi in P uptake, the relationship between the VAM condition and photosynthesis is of particular interest. In soybeans, the rate of net $CO_2$ exchange (CER) was higher in VAM plants than in P-supplemented nonVAM plants of equivalent dry mass, regardless of the source (nodules or fertilizer) of N (Brown and Bethlenfalvay 1987). Nodule activity, however, was significantly higher in nonVAM plants. Photosynthetic P- and N-use efficiencies (CER/unit mass of leaf P or N) were significantly higher in VAM than in nonVAM plants, suggesting a nonnutritional effect of the fungal endophyte on chloroplast activity (Brown and Bethlenfalvay 1988). Examination of the carbon economy of the tripartite soybean association (Harris *et al.* 1985) showed that increased C demand by the endophytes was met by an increase in the rate of $^{14}CO_2$ fixation by the symbiotic plants. Microsymbiont interactions thus appear to be mediated, to some extent, by C assimilation and allocation by the host.

## STRESS

Water-status is altered in soybean by VAM colonization (Nelsen 1987), promising potential benefits in arid regions by influencing the host plant's tolerance to drought (Busse and Ellis 1985). Although transpiration and leaf conductance were shown to be higher in unstressed VAM soybeans than in noncolonized plants of comparable nutritional status, water loss was shown to converge with increasing stress in the two treatments, while nodule activity was significantly higher in the stressed, colonized plants (Bethlenfalvay *et al.* 1987). The uptake of soil water by VAM plants at soil water potentials below the permanent wilting point of nonVAM plants, and the demonstration of direct (not P-nutrition mediated) VAM effects on plant water status under drought conditions (Bethlenfalvay *et al.* 1988a), point to the special role of the VAM association in stress alleviation (Fitter 1986). Salt-stress alleviation has not been reported in soybeans, but increased tolerance of other VAM-colonized crop plants (Pond *et al.* 1984) suggests its occurrence. Alleviation of heavy metal toxicity has been reported (Bethlenfalvay and Franson 1988, Dueck *et al.* 1986), but the mechanisms are obscure.

As agents of biological stress reduction, VAM fungi have been shown to deter or reduce the effects of some pathogens on the host (Schenck 1981). Unfortunately, the effect is not uniform, and deleterious effects of VAM-fungi have also been observed (Davis and Menge 1980). The impacts of host, symbiont, pathogen and environment must all be considered in the evaluation of the influence of VAM fungi on plant disease (Dehne 1982). The reactions of mycorrhizae to plant-protection chemicals have been reviewed (Trappe *et al*. 1984, Vyas 1988) and the effects of nontreated or surpressive field soils on mycorrhizae investigated (Ross 1980).

## HOST-ENDOPHYTE COMPATIBILITY

Although VAM fungi are not host-specific, soybean cultivars may be differentially colonized by indigenous populations of VAM fungi (Heckman and Angle 1987), may show different growth and yield responses to various fungal species (Carling and Brown 1980), or the fungi themselves may develop differently under the host's influence (van Nuffelen and Schenck 1983). We hypothesize that co-evolution of host and endophyte in a given edaphic and environmental setting produces biochemical and ecophysiological mechanisms of preference which are only partially or incompletely satisfied when a plant is transferred from its center of native adaptation (Simmonds 1984) to new areas of agricultural utilization. Co-introduction of VAM fungi from the host's native habitat should be attempted for maximizing production and protection effects.

## PLANT-SOIL RELATIONS

No account of the VAM symbiosis would be complete without a mention of its potential effects on soil stability (Bethlenfalvay *et al*. 1988b). There is a growing body of literature concerned with this subject which has been briefly reviewed recently (Ames and Bethlenfalvay 1986). Mention of the involvement of VAM fungi in soil biology and physics may now be found in a number of in-depth treatments of the subject (Tinsley and Darbyshire 1984, Lynch 1983).

## CONCLUSION

The VAM fungus is an integral part of the healthy soybean plant under natural conditions. Its effects on the morphology and physiology of its host plant and host soil are pervasive. Its modes of action on the host, apart from that of P nutrition, are little known. Selection of compatible combinations of host cultivars and VAM-fungal and rhizobial isolates adapted to the edaphic conditions of their respective sites promises improvements in crop production and protection.

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