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Review

Vesicular-arbuscular mycorrhizae in relation to plant disease

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Vesicular-arbuscular mycorrhizae (VAM) enhance plant growth through increased nutrient uptake, stress tolerance and disease resistance. As an integral part of the root system, they interact with other microorganisms in soil and result in increased root exudation approaching about 25% of the plant dry matter production. Roots support a multitude of microorganisms that, in concert, can have profound influence on growth and survival of the plant. VAM fungi can alter the root exudation pattern, enhance chitinolytic activity and alter photosynthetic/respiratory deficiencies. VAM-positive plants are known to exhibit varied resistance towards soil-borne and foliar pathogens. The known interactions include a number of mechanisms, such as exclusion of the pathogen, lignification of plant cell walls, changed phosphate nutrition resulting in altered exudation by roots, and formation of inhibitory low molecular weight compounds. The purpose of this review is to discuss VAM–plant–pathogen interactions and the possible mechanisms involved in altered resistance. Based on these observations, a working model is proposed to explain the VAM–disease interaction under varied environmental conditions.

Key words: Fungi, pathogens, root exudation, soil-borne disease, suppression, vesicular arbuscular mycorrhizae.

Besides increasing uptake of phosphate, vesicular-arbuscular mycorrhizae (VAM) improve plant resistance to various abiotic and biotic stresses. However, what specifically contributes towards altered plant resistance is not properly understood. For example, VAM-positive plants are less susceptible to pathogens but complete resistance is not conferred. With respect to the VAM–pathogen relationship, enhanced severity of foliar disease has been described but a near-neutral response also occurs (Dehne 1982). The known interactions are, therefore, likely to include a magnitude of mechanisms comparable with fungal pathogenesis (Gianinazzi–Pearson & Gianinazzi 1989). Altered host susceptibility towards the pathogen and changed 'mycorrhizosphere' have been implicated. It is also important that, in evaluating these interactions, the processes by which the symbiont changes or inhibits the pathogen are differentiated.

The latest developments in the emerging research area of VAM–pathogen interactions are reviewed here, with emphasis on the mechanisms of pathogen resistance. We propose, in this review, a working model to serve as a guide for testing VAM influence in relation to plant disease under a variety of soil and environmental conditions.

VAM–Plant Disease Responses

Interactions of VAM with rhizosphere microorganisms have received considerable attention and a variety of responses have been described (Tables 1 and 2). Broadly these can be summarized as follows:

(1) VAM infection, in general, protects plants from soil-borne fungi.
(2) Higher nutrient concentrations in mycorrhizal plants make such plants more susceptible to foliar pathogens.
(3) No definite relationship appears to exist between bacterial infection and mycorrhization.
(4) Pre-mycorrhizal infection of transplanting crops protects the plants from nematode infection.

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Table 1. Influence of vesicular-arbuscular mycorrhizae (VAM) on pathogenic fungi.*

Fungus	Host plant	Reference
Aphanomyces euteiches	Pea	Rosendahl 1985
Fusarium avenacium	Clover	Dehne 1982
F. oxysporum f.sp. *radicis lycopersici*	Tomato	Carnon *et al.* 1986
F. oxysporum cepa	Onion	Dehne 1982
F. solani	Soybean	Zambolim & Schenck 1983
Gaeumannomyces graminis var. *tritici*	Wheat	Graham & Menge 1982
Macrophomina phaseolina	Soybean	Krishna & Bagyaraj 1983
P. drechsleri f. sp. *cajani*	Pigeonpea	Bisht *et al.* 1985
Pythium aphanidermatum	Tomato	Hedge & Rai 1984
Sclerotium rolfsii	Peanut	Krishna & Bagyaraj 1983
Thielaviopsis basicola	Tomato	Giovannetti *et al.* 1991
	Onion	Dehne 1982

* Disease incidence in all fungus–host combinations was reduced by VAM treatment.

Table 2. Influence of vesicular-arbuscular mycorrhizae on nematodes.

Nematode	Host plant	Disease incidence*	Reference
Meloidogyne arenaria	Peanut	+	Hussey & Roncadori 1982
Meloidogyne haplia	Tomato	–	Cooper & Grandison 1986
	Alfalfa	–	Grandison & Cooper 1986
Meloidogyne incognita	Soybean	–	Kellam & Schenck 1980
	Cotton	–	Saleh & Sikora 1984
	Cotton	–	Smith *et al.* 1986
Paratylenchus penetrans	Pigeonpea	+	Elliott *et al.* 1984
Radopholous citrophilus	Rough lemon	–	Smith & Kaplan 1988
Rotylenchus reniformis	Cotton	–	Sitaramaiah & Sikora 1982

* +—increase; ——decrease.

Mechanism of Suppression of the Pathogen by VAM

The operative mechanisms can be differentiated into physical, physiological and biological.

Physical Mechanisms

Lignification is reported to prevent penetration of mycorrhizal plants by *Fusarium oxysporum* (Dehne & Schoenbeck 1978). A stronger vascular system in mycorrhizal plants increases flow of nutrients, imparts greater mechanical strength and reduces the effect of vascular pathogens (Schoenbeck 1979). Smaller syncytia with fewer cells confer resistance of the host against nematodes (Fassuliotis 1970).

Physiological Mechanisms

Nutritional Changes. The host–pathogen relationship is influenced indirectly through physiological alteration and competition for space and/or host resources. Through increased phosphate nutrition, VAM fungi enhance root growth, expand the absorptive capacity and affect cellular processes in roots (Hussey & Roncadori 1982; Smith & Gianinazzi-Pearson 1988). Such induced compensatory process may explain increased tolerance of the mycorrhizal and P-fertilized plants towards the pathogen (Wallace 1973); greater tolerance is also attributable to increased root growth and phosphate status of the plant (Cameron 1986).

Phosphate and root isoflavonoid accumulation by VAM appear distinct responses. The nutritional effect of VAM does not seem to be directly implicated in increased isoflavonoid content of the mycorrhizal roots (Morandi *et al.* 1984).

In addition to phosphate, VAM enhance uptake of Ca^{2+}, Cu^{2+}, SO_4^{2-} and Zn^{2+} (Smith & Gianinazzi-Pearson 1988). Host susceptibility to infection and tolerance to disease is influenced by the nutritional status of the host and fertility level of the soil (Wallace 1973; Cook & Baker 1982). For example, nematode-damaged plants frequently show deficiency of boron, nitrogen, iron, magnesium and zinc (Good 1968). In the absence of VAM, phosphate can combine with minor elements to create deficiencies which would pre-dispose plants to root-knot nematodes (Smith *et al.* 1986).

Biochemical Changes. Available evidence demonstrates an intimate relationship between root exudation and disease initiation (Cook & Baker 1982). Influence of VAM and phosphate nutrition on exudation as a regulatory process in root disease has been investigated (Graham & Menge 1982). Higher amounts of amino acids, especially arginine, found in root exudates of mycorrhizal plants, reduced chlamydospore production in *Thielaviopsis basicola* (Baltruschat & Schoenbeck 1975). Tomato roots inoculated with *Glomus fasciculatum* had increased concentrations of phenylalanine and serine; these two amino acids being inhibitory to root-knot nematode development (Parvatha Reddy 1974). Higher amounts of catechols, which inhibit *Sclerotium rolfsii* growth *in vitro*, have been reported in mycorrhizal roots (Krishna & Bagyaraj 1986).

Restricted VAM infection in root tissue suggests involvement of suitable chemical signals from the host to the symbiont and vice-versa. Recent studies show that the process of VAM infection resembles that of obligate fungal pathogens and the host response, in legumes at least, is governed by genetic mechanisms to those that operate in *Rhizobium* infection (Wyss *et al.* 1990).

Increased peroxidase, localized mainly in the vacuole and cell wall, and phytoalexins (glyceollin, coumestrol) have been conclusively documented in VAM-positive plants (Morandi *et al.* 1984). Enhanced accumulation of coumestrol in soybean helps explain how mycorrhizal infection decreases the development of pathogenic nematodes more consistently than that of fungi (Kellam & Schenck 1980; Hussey & Roncadori 1982). Accumulation of isoflavonoids suggests activated metabolism involving *de novo* synthesis of enzymes. Thus, plants infected with VAM fungi are likely to be more resistant to subsequent attack by pathogenic fungi and nematodes. Using more sensitive immunocytochemical techniques, Gianinazzi-Pearson *et al.* (1988) have reported localization of specific proteins within the host cells containing living arbuscules. These observations indicate that certain mechanisms involved in host resistance are activated when roots are infected by VAM fungi. The level of expression, however, appears sufficiently weak to be compatible with the permanent biotrophic relationship between the two partners.

Biological Mechanisms
Because of their impact on host physiology, VAM fungi exert a selective pressure on the microbial population in the mycorrhizosphere; some of this can result in specific effects on root pathogens. For example, Meyer & Linderman (1986) showed that sporangium and zoospore production by the root pathogen *Phytophthora cinnamomi* was reduced in the presence of rhizosphere leachates from VA mycorrhizal sweet corn and chrysanthemum. According to Secilia & Bagyaraj (1987), pot cultures of *Glomus fasciculatum* harboured more actinomycetes antagonistic to *Fusarium solani* and *Pseudomonas solanacearum* than VAM-negative controls or other mycorrhizal fungal species.

Proposed Model for Relationship Between VAM and Soil-Borne Diseases

Based on our current understanding of the role of VAM in plant disease, a model is proposed that takes into account soil and environmental factors, plant vigour and intensity of VAM infection. This obviously is an over-simplification of the complex interactions but should provide a working base to make a realistic assessment of the role of VAM, especially in soil-borne plant diseases.

Low Disease Severity
Situation I:

(a) VAM strain is effective and present in soil at optimum dose level.
(b) Susceptibility of host towards VAM is high.
(c) Environmental and soil factors favour VAM development.
(d) Pathogen dose is moderate.

In view of the high VAM infection, the disease severity will be low, resulting in improved host vigour without loss in yield.

Moderate Disease Severity
Situation I:

(a) VAM strain is effective, resulting in high root infection.
(b) Environmental and soil factors support VAM infection.
(c) Pathogen population is high.

Under the above conditions, although the availability of the pathogen is high, yield loss would be marginal due to high VAM infectivity and normal host vigour.

Situation II:

(a) Moderate susceptibility of host towards VAM.
(b) Soil and environmental factors favour VAM infection.
(c) Pathogen density is low.

In spite of favourable soil and environmental factors, the above situation will lead to slight loss in yield because VAM proliferation is not extensive and host vigour is moderate.

Situation III:

(a) There is moderate susceptibility of host towards VAM.
(b) Soil and environmental factors are favourable.
(c) Effective pathogen population is high.

The above condition will lead to loss in host vigour, causing moderate yield loss.

Situation IV:

(a) There is high susceptility of the host towards VAM.
(b) Environmental conditions are favourable.
(c) Soil conditions are only partially supportive.
(d) Pathogen population density is not high.

One would expect only marginal yield loss under the above condition, as the vigour would be normal.

While the above four situations explain slight or moderate loss in yield there can be another set of conditions which would lead to high disease severity. The latter is described below.

High Disease Severity
Situation I:

(a) There is high susceptibility of the host towards VAM.
(b) Soil and environmental factors are unfavourable leading to low VAM infection.
(c) Pathogen population is high.

These conditions would lead to low host vigour and result in high loss in yield.

Situation II:

(a) Moderate susceptibility of the host towards VAM.
(b) Soil conditions are unfavourable and lead to low VAM infection.
(c) Environmental factors are favourable.
(d) Pathogen population is high.

The host vigour will decrease under these conditions, resulting in high loss in yield.

Conclusions and Future Perspectives

The foregoing discussion would be meaningless if certain conclusions and future projections are not drawn so that planned exploitation of VAM–disease interaction is possible. Greater attention needs to be placed on the evaluation of the level of inoculum required for combating a particular disease. Species- or isolate-specific screening of VAM–plant combinations needs to be carried out for each pathogen in question. Techniques of VAM application in field must be standardized.

A low level of fungal aggressiveness and a weak plant reaction are two factors that permit establishment of a symbiotic relationship (Gianinazzi 1984). A weak but permanent activation may explain enhanced resistance of VAM plants to certain soil-borne pathogens (Bagyaraj 1984). In this respect, the following specific questions still need to be answered:

1. How do VAM induce the production of chemicals? Does the mycorrhizal fungus produce elicitors or does it perturb root tissues so that a plant elicitor is liberated?
2. Do roots of VAM-positive plants produce these chemicals in a manner comparable with VAM-negative plants when challenged by a soil-borne pathogen?
3. Where are such molecules produced in the root system?

In arriving at the above goals, current technological advances can provide the necessary back up. For example, immunology offers the precision of recognition by monoclonal antibodies. The use of suppressants can permit selection of antibodies to unique features of mycorrhizal fungi. Such procedures have already demonstrated differences between races of the fungal pathogen *Phytophthora megasperma* (Ayers *et al.* 1986) and, to a limited degree, between species of fungi in wheat bunt (Banowetz *et al.* 1984). Partial differentiation between spores of VAM fungi has been achieved by the use of polyclonal antibodies to a specific structural component or the enzymes of a germinating fungus; expression of this factor in mycorrhiza can be detected using ELISA. Probing with cDNA has been used to determine the pattern of induction for enzymes of phenolic biosynthesis in plant defence responses against microbial pathogens (Cramer *et al.* 1985) and would appear suitable for further dissection of VAM–pathogen interactions.

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