

PESTICIDE
INTERACTIONS
in
CROP
PRODUCTION

Beneficial *and* Deleterious Effects

Edited by

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studied to date did not affect VAM fungi, and some of them, such as aldicarb and DBCP, may increase VAM development.^{3,4,35,44} Whether the positive effect of aldicarb on VA mycorrhizal colonization operates through the elimination of competitive nematodes or whether it directly affects the physiology of the fungus or root have yet to be demonstrated. However, in the absence of nematodes, either no effect or a slight decrease in VA colonization has been observed.^{35,50} These results suggest that the beneficial effect of aldicarb on VAM symbiosis is traceable to its effect on the nematode population. DBCP seems to have the same mechanism of action.^{29,114,117}

On the other hand, some fungicides such as metalaxyl and captan do not inhibit VA colonization. Metalaxyl is an acylalanine systemic fungicide active against some *Oomycetes*. The application of metalaxyl at realistic usage rates resulted in increased VAM colonization in several plants or in no change in VAM colonization.^{5,138-140} However, metalaxyl treatment did not increase vesicle numbers or chlamydospore production.⁵ In fact, in some experiments the VA colonization of root, as well as the growth of mycorrhizal plants, were reduced by metalaxyl, although the mechanism by which this fungicide inhibits VA colonization is not yet understood.³⁴ Captan is generally considered to have no effect on spore germination, hyphal growth, or VAM colonization.^{24,28,29} However, at the recommended agricultural level or at higher doses, captan had deleterious effects on VAM fungi, as evidenced by reduced root colonization, metabolic activity of the fungus colonizing the roots, extramatrical chlamydospore numbers, and numbers of infective propagules, regardless of the species of VAM fungus, which colonized the roots.^{17,29} This effect was less intense in comparison with other fungicides, and at half the recommended level, captan increased all mycorrhizal parameters in comparison to controls.^{5,15,17} The beneficial effects of metalaxyl and captan on VAM are probably due to the reduced competition for space and nutrients between VAM fungi and other microorganisms such as *Phytophthora*, rather than to any effect on the VAM fungi.^{15,17,139} However, the application of other fungicides such as benomyl can reduce the level of antagonism induced by the symbiont on parasitic nematodes and may therefore compromise the level of biological control attained in the absence of fungicides.²²

V. CONCLUSIONS AND FUTURE TRENDS

Studies of the effects of pesticides on the VAM association continue to yield variable results. Thus, it is almost impossible to establish a general mode of action for different pesticides, owing in part to the great variety of crops, soils, and environmental conditions under which pesticides have been studied.⁴ The application of different commercial preparations of the same pesticide can modify the effects of the pesticide because of differences in the detergents and surfactants often added to the product to increase its wettability. The use of soil-free or root-free media may be suitable for testing the effect of pesticides applied as purified inert ingredients, because fewer variables need to be considered.^{39,41} These techniques may be sensitive enough to detect differences in susceptibility to pesticides among species and even among strains of VAM fungi.^{39,41} Although these studies may be of use in physiological experiments, the results obtained with these methods cannot be extrapolated to field conditions, because it appears that fungi exposed in a soil-free or root-free media are much more sensitive to pesticides than fungi in soils or in an established mycorrhizal formation in host roots.^{39,41} The results of pot trials with pesticides should also be viewed with care because of the known "cycling" effect of pesticides under these conditions, which can result in artificially high concentrations of pesticide in the root zone.⁴⁶

The diversity of interaction between VAM and plant pathogens means that generalizations as to how the presence of a VAM fungus reduces the population of the pathogen and/or the severity of the disease must be made with caution. However, three general mechanisms by which VAM may protect plants against pathogens can be suggested: (1) a general, quick, rapidly induced mechanism at the rhizosphere level; (2) a systemic induction of resistance against the parasitic pathogen; and (3) improved plant vigor owing to enhanced plant nutrition and/or increased concentrations of parasite-inhibiting substances. Most research has been focused on the third aspect.

The effect of pesticides on microorganisms which accompany VAM fungi in the inoculum or in field soils may explain the different effects observed with the same pesticide by different authors. However, this aspect remains to be investigated in depth.

has also been described.^{83,125} Some authors still are unable to find appreciable increases in the production of chitinase and peroxidase involved in the formation of the phenols lignin and suberin in roots colonized by VAM fungus.¹²⁶⁻¹²⁸ Morandi and Bayley¹²⁹ observed increased concentrations of the phytoalexins glyceollin I, coumestrol, and diazein in VAM-colonized soybean plants. They interpreted this accumulation of isoflavonoids as an indication that mycorrhizal plants respond more quickly to attack by pathogenic fungi and nematodes than do nonmycorrhizal plants. Recent observations show, however, that the levels of glyceollins were very low in *G. mosseae*-colonized roots and that these isoflavonoids were formed only at late stages of VA root colonization.^{130,131}

The primary effects of VAM fungus in reducing disease severity have been associated with improved P nutrition.^{68,88,122} It has been described that VAM did not increase the resistance or tolerance to plant pathogens unless mycorrhizae conferred a P nutritional advantage over the non-mycorrhizal plant.⁷⁴ High P levels in the VAM host plant raised amino acid and sugar content and reduced root exudation, especially sugars, with a subsequent decrease in disease severity.^{99,132} However, some authors could find no relationship between the level of sugars in root extracts and root exudates and the degree of VAM colonization.^{133,134} Other authors concluded that improved P nutrition was not responsible for the increased resistance of plants.^{66,84,86} VAM fungi may increase host tolerance to pathogens by increasing the uptake of essential nutrients other than P that would be deficient in a nonmycorrhizal plant. Nematode-damaged plants are frequently deficient in B, N, Fe, Mg, and Zn,⁵⁸ although some reports indicated that nutrient levels had no significant effect on the number of nematodes.^{95,96} The mechanisms of tolerance appear to be related not only to the nutritional superiority associated with colonization by the mycorrhizal fungi, but also with other factors connected with VA mycorrhizal fungi.^{66,80,86,89,91} In fact, the ability of VAM fungi to reduce the negative effects of pathogens was observed regardless of the extent of VAM colonization and growth effects.^{66,89,91} On the other hand, VAM protected tomato plants against the pathogenic effect of bacteria, fungi, and nematodes when both the VA fungus and the plant pathogen were inoculated at the same time, i.e., when the effect of the mycorrhiza was unlikely to operate via host nutrition or a general change in host plant physiology induced by the establishment of symbiosis.^{54,64,89,91,98,99,106,117,118} This suggests a direct interaction between the VAM fungus and the pathogen in the extramatrical phase of the former. Although it has been suggested that the pathogen could be inhibited directly by the VAM fungus by compounds released from the VAM spores or mycelium,⁸⁹ this protective mechanism remains untested. Such a protective effect may also result from the induction of inhibitory metabolites in the host plant in response to VA initiation. As VAM fungi are slow colonizers of roots compared to most pathogens, root infection by pathogens normally precedes VAM root colonization, hence, their potential benefit may be preempted by VAM fungi when roots are exposed to both microorganisms at the same time. In this sense, alterations in plant roots by soluble and volatile messengers from the VAM mycelium before the fungus penetrates the root have been observed.^{135,136} Direct interaction between VA fungi and the pathogen in the absence of the plant has not been studied.

IV. PESTICIDE-PATHOGEN-VAM INTERACTION

Because VAM fungi and root pathogens commonly occur together in the roots and rhizosphere of the same plant, pesticide application affects both organisms. However, few studies have examined the effect of pesticides on VAM through their effects on plant pathogens.

Soil fumigation with methyl bromide negatively affected VAM and killed most living soil organisms, including some beneficial microorganisms such as bacteria and actinomycetes, which may improve VAM colonization.² Crop growth response and percentage colonization of plants inoculated with VAM were often higher in fumigated soil than in natural soil, even though the application of fumigants reduced or eliminated indigenous VAM fungi.^{9,14} One possible cause of reduced root colonization by indigenous VAM fungi in some natural soils is that pathogens compete with VAM fungi for specific niches. Many pathogens reduce mycorrhizal root colonization, and removal of these pathogen as competitors may improve VAM colonization in natural soils. The pathogens which most significantly reduce VA mycorrhizal root colonization are nematodes and fungi. The use of nematicides and fungicides which eliminate pathogens without affecting VAM fungi will help to increase plant growth. Most nematicides

per plant). This beneficial effect disappeared when the inoculum of nematodes was high (200 eggs per plant).⁹⁴ With increasing inoculum density of the nematode *M. javanica* (0 to 10,000 eggs per plant), the bean plant growth was reduced, but there was no effect on mycorrhizal colonization or chlamyospore production by *G. etunicatum*. The presence of the fungus decreased nematode egg production.¹⁰⁶

Fewer galls and nematode cysts of *M. javanica* were observed in bean and tomato roots colonized with *G. fasciculatum* and *G. etunicatum*, respectively.^{95,99,106} *G. etunicatum* negatively affected the nematode and increased bean growth even when both organisms were inoculated at the same time.

In studies of interaction between VAM and nematodes of the genus *Heterodera*, these two organisms were at times mutually inhibitory, and competition between the nematode *H. solanacearum* and the fungus *G. gigantea* was observed.¹⁰⁷ The fungus interfered with nematode reproduction and competed for space. In other investigations with the nematodes *H. avenae* and *H. schachtii*, the only finding of significance was *Endogonaceae* spores inside empty nematode cysts,¹⁰⁸ indicating that the two organisms competed for space only, the empty nematode cysts providing space for *Endogonaceae* sporulation. In other experiments, spores of VAM have been found inside female preadult nematodes; hence, the competition between the two organisms cannot be explained solely in terms of space limitations.¹⁰⁸

There are few studies of the interaction between VAM and nematodes belonging to the genera *Globodera*, *Radopholus*, *Rothylenchulus*, *Pratylenchus*, and *Tylenchulus*, but in general, VAM protects plants against the action of these pathogens.¹⁰⁹⁻¹¹² *P. penetrans*, however, reduced colonization by *G. fasciculatum* in bean, and *Scutellonema cavenessi* decreased colonization of *G. mosseae* in soybean.^{113,114}

C. BACTERIA

Few reports deal with plant susceptibility to bacterial pathogens in relation to the incidence of VA fungi, and conflicting results have been obtained. The susceptibility of peach plants to the bacterial canker caused by *Pseudomonas syringae* was not affected by VAM colonization,¹¹⁵ but a reduction in the severity of bacterial wilt caused by *P. solanacearum* was found in VAM-colonized tomatoes.¹¹⁶ *G. mosseae* protected tomato plants against the pathogenic effect of *Erwinia carotovora* and *P. syringae* when the VAM fungus was inoculated before or at the same time as the pathogenic bacteria. *E. carotovora* and *P. syringae* depressed the dry matter weight of nonmycorrhizal tomato plants, but neither the dry weight of VA mycorrhizal plants nor the percentage of root length showing VA colonization were reduced by the pathogenic bacteria. The reduction in the population of *E. carotovora* and *P. syringae* in the rhizosphere of VAM-colonized plants was observed regardless of P concentration in plants.^{61,117,118}

D. VIRUS

Another little-studied area is the interaction between VAM and viruses. All experiments to date showed that VAM increased the susceptibility of plants to viral diseases. However, VA fungus did not absorb viral particles and did not act as a vector for the virus.¹¹⁹ Although viral infection produced more severe symptoms in plants colonized by VAM fungi, these plants appeared to grow more vigorously. These results were attributed to the higher levels of P in VAM-colonized plants.⁵⁶

E. MECHANISMS OF ACTION OF VAM ON PLANT PATHOGENS

The mechanisms proposed to explain VAM fungal effects on soil-borne plant pathogens have generally been based on morphological and physiological changes induced in the plant by the VAM fungus.⁵⁵⁻⁶¹ The greater tolerance to disease observed in VA mycorrhizal plants has been attributed to increased root growth,⁹³ increased cell wall thickness,¹²⁰ and increased strength of the vascular system.¹²¹ Competition between VAM fungus and plant pathogens for space or infection sites has also been suggested.^{93,122} Several authors, however, have suggested that competition for available photosynthates or the conversion by VAM fungus of host carbohydrates into forms not usable by the pathogen may be more important than competition for space,^{86,103} but this hypothesis has yet to be tested.

Another proposed mechanism of action involves increased production of several plant components such as amino acids, lignins, and phenols in response to root penetration by the VAM fungi, resulting in protection of the root system against pathogens by other component such as arginine,⁸¹ phenylalanine and serine,⁹⁹ lignin,¹²⁰ chitinase,¹²³ and the phenols, including ortho-dihydroxy phenols and cinnamoyl amides.^{88,120,124} The production of other antiparasitic substances which can be released in root exudates

pea at the same time. When the VA fungus was inoculated into peanut, cucumber, peach, and grain before or simultaneously with *Sclerotium rolfsii*, *Pythium ultimum*, *Cylindrocarpon destructans*, and *Cochliobolus sativus*, respectively, VAM were able to reduce disease intensity and to increase survival of the plants.⁸⁸⁻⁹¹

B. NEMATODES

VAM can limit the population of nematodes and increase growth of plants infected by these pathogens.^{92,93} The response of the interaction between both organisms depends on the host plant, VA and nematode strains, inoculum density, plant susceptibility to nematodes, and soil fertility.⁹⁴⁻⁹⁷

The interaction between VAM and nematodes belonging to the genus *Meloidogyne* has been the subject of many studies.⁹⁶ Carrot, clover, cotton, oat, onion, soybean, tobacco, and tomato inoculated with VAM fungi belonging to genus *Glomus* or *Gigaspora* showed increased resistance to the action of the nematodes *M. incognita* and *M. hapla*, and few larvae developed into adults in mycorrhizal plants.^{92,98-100} In contrast, VAM may leave unaffected, or even increase, the population of endoparasitic nematodes in cotton, peach, and tomato.^{96,97,101}

The interaction between VAM and the nematodes *M. incognita* and *M. hapla* can be affected by the time interval at which they are inoculated. Clover, cotton, oat, onion, peach, tobacco, and tomato plants preinoculated with VAM (*G. mosseae*, *G. fasciculatum*, and *G. intraradices*) were more resistant to the action of nematodes, and VAM usually decreased nematode development and egg production more effectively than when both organisms were inoculated at the same time.^{92,93,98,99} On the other hand, when *M. incognita* and *G. macrocarpum* were inoculated simultaneously in soybean and cotton, VAM eliminated the damage caused by the nematode, but the production of eggs increased in mycorrhizal plants because VAM increased the root volume and thus the number of roots susceptible to the nematode.^{96,102} Percentage colonization of tomato by *G. fasciculatum* was also reduced when *M. incognita* was inoculated before or at the same time as the fungus, but not when inoculated after the fungus.⁹⁹ The mycorrhizal fungus *G. fasciculatum* did not significantly alter *M. incognita* number or egg production 30 d after simultaneous inoculation, but later, when the fungus was well established, both nematode densities and egg numbers were reduced and a positive relationship was observed between the level of fungal root colonization and antagonism to *M. incognita* in cotton.^{72,103} However, the tolerance of susceptible alfalfa cultivars to infection and the development of *M. hapla* were similar when plants were precolonized with the VA fungus and when both organisms were inoculated at the same time.⁵⁴ Inoculation with VAM increased plant growth and reduced the number and development of adults of *M. hapla* in root.⁵⁴

Different VA endopytes can differentially affect the reproduction of nematodes. *G. heterogama*, *G. calospora*, and *G. macrocarpus* in soybean, and *G. margarita*, *G. eutunicatum*, and *G. mosseae* in cotton stimulated nematode density when coinoculated with *M. incognita*.^{93,104} Nevertheless, the number of eggs per plant did not increase in plants colonized by *G. eutunicatum* or *G. mosseae*, despite the higher root dry weight of VA-colonized plants compared with non-VA-colonized plants. However, *G. margarita* did not affect the number of nematode eggs per gram of root. This indicates that *G. mosseae* and *G. eutunicatum* increased plant resistance to the nematode, and that *G. margarita* made the plant more tolerant to infection by the nematode.^{93, 104}

Host-nematode relationships are affected by differences between host cultivars. Inoculation of alfalfa plants with VAM fungi seems to increase the resistance of nematode-susceptible alfalfa cultivars and enhances the resistance of resistant cultivars to the nematode *M. hapla*.⁵⁴ The percentage colonization by *G. margarita* was greater in resistant cultivars of coffee infected with *M. exigua*, whereas VA colonization was reduced by nematodes in susceptible coffee cultivars.¹⁰⁵

Nutrient level had no significant effect on the numbers of nematodes, but increasing soil fertility diminished the beneficial function of the fungus.^{95,97}

On the other hand, the nematode *M. arenaria* obviates the beneficial effect of *G. fasciculatum* in grape.⁹⁴ This nematode, however, did not affect growth of peanut plants colonized with either *G. eutunicatum* or *G. margarita*.

The number of nematodes in the soil can play an important role in biological control by VAM, as the presence of VAM increased plant growth when the population of *M. arenaria* was low (200 eggs-

III. INFLUENCE OF VAM ON INTERACTIONS WITH PLANT PATHOGENS

Because VAM fungi and root pathogens commonly occur together in the roots and rhizosphere of the same plant, the potential role of mycorrhizae as biocontrol agents has recently received considerable attention.^{54,61}

A. FUNGI

The VA colonization of tomato by *G. etunicatum* improved the penetration and development of the pathogenic fungus *Fusarium oxysporum*.⁶² However, when tomato and other plants were previously colonized by *G. mosseae*, *G. intraradices*, *G. macrocarpum*, *G. fasciculatum*, and *G. tenuis*, the severity of *F. oxysporum* infection was reduced regardless of the method of inoculation of the fungal pathogen or its population level.⁶³⁻⁶⁵ However, the intensity of the disease depended on the substrate where the symbiosis was developed.⁶⁴ On the other hand, *F. oxysporum* did not affect the colonization of plant root by *G. intraradices*, *G. fasciculatum*, and *G. tenuis*.^{65,66}

VAM did not reduce the pathogenic action of *Gaeumannomyces graminis*.⁶⁷ However, when a small number of pathogens were inoculated in soil deficient in P, VAM reduced the severity of *G. graminis* infection in wheat, this effect being similar to that produced by the application of P.⁶⁸

Considerable variability in the interaction between VAM and pathogenic fungi of the genus *Phytophthora* has been observed. In fact, soybean colonized with *G. caledonicum* or with *G. mosseae* was more resistant to *Ph. megasperma* than non-VA-inoculated controls.^{69,70} Some soybean plants infected by the pathogenic fungus were able to develop VA mycorrhizas, which indicates that the development of VA colonization was unaffected by the presence of the pathogenic fungus.⁷⁰ However, greater damage was caused by *Phytophthora* in plants colonized with a chlamydo-spore species of *Endogonaceae*: 33% of mycorrhizal-colonized plants died, whereas all non-VA-colonized plants were alive.⁷¹ This effect occurred because the strain of *Endogonaceae* (possibly *Glomus*) used in these experiments had large chlamydo-spores which could distort the root, making it more susceptible to the pathogenic fungus. VAM induced some resistance to the pathogenic effect of *Ph. parasitica* in citrus plants. However, this effect seemed to depend on the level of the pathogenic population, as inoculation with *G. fasciculatum* did not protect citrus, alfalfa, and avocado plants when the population of *Ph. parasitica* was high,⁷² but when the population level of *Ph. parasitica* was lower (20 chlamydo-spores per gram of soil), VAM protected plants against this pathogen.⁷³ However, *G. intraradices* did not increase the resistance or tolerance of citrus to *Phytophthora* root rot unless mycorrhizae conferred a P nutritional advance over the non-mycorrhizal plant.⁷⁴ Moreover, no interaction between VAM and *Ph. fragaria* in *Fragaria vesca* and *Ph. palmivora* in papaya was found.^{75,76} The interaction between *Ph. cinnamoni* and VA endophytes was also variable, and interactions have been described in which VA mycorrhizas protect,⁷⁷ made plants more susceptible to,⁷² or had no effect on infected plants.⁷⁸

The presence of VAM in onion root increased the resistance of this species to the action of *Pyrenochaeta terrestris* when the pathogen population was low.⁷⁹ In the same way, common root rot disease caused by *Bipolaris sorokiniana* in barley was suppressed by VAM fungi.⁸⁰ The action of VAM on both fungal pathogens seem to be direct, as in individual roots of the same plants, and the pathogen was more effectively restricted in the roots which were mycorrhizal.^{79,80}

VAM plants are more resistant to the stress produced by the pathogen *Thielaviopsis basicola*. Mycorrhizal plants were able to inhibit the production of chlamydo-spores of the pathogen.⁸¹⁻⁸³ However, in citrus there was no significant reduction in the severity of *T. basicola* infection.⁸⁴

Experiments designed to study the interaction between VAM and *Verticillium dahliae* failed to show differences in plant growth in cotton.⁸⁵ However, increased severity of the disease as measured by vascular discoloration or the number of propagules of *Verticillium* in the petiole tissue was found. This effect was attributed to the higher P nutrition of VAM plants, as similar results were observed in plants fertilized with P. No effect of VAM against the action of *Verticillium* was observed in tomato.⁸⁶

Previously colonized pea plants were more resistant to the action of *Aphanomyces euteiches*.⁸⁷ However, there was no reduction in plant pathogens when both microorganisms were inoculated into

medipham, sulfalate, and triallate were found to have little detrimental effect on the VAM symbiosis.^{4,38,39} However, a higher dose (or a repetition of the recommended dose) of the herbicides alachlor, cyanazine, 2,4-D, diallate, diquat, dinoseb, MCPA, paraquat, prodiamine, propachlor, simazine, and trifluralin induced a significant reduction in plant colonization by VAM fungi.^{4,38-43} Other herbicides such as chlortoluron, linuron, mecoprop, and eptam negatively affect VAM symbiosis, even at recommended rates.^{39,44}

Herbicides can affect VA fungi either directly or through their effects on plants. Several of the above-named herbicides are inhibitors of photosynthesis and would be expected to affect VAM colonization through their effect on the plant. However, other photosynthesis-inhibiting herbicides have no effect on VA mycorrhizas despite their ability to decrease metabolic activity of the fungus, sugar content in the root, and plant growth.³⁸ More recent studies indicated that some herbicides can affect VA fungi directly; chlortoluron, difenzoquat methyl sulphate, MCPA, mecoprop, and oxadiazon affected VA colonization by some individual fungal species or strains, but not by others, without affecting plant growth.^{39,41,45,46}

However, it is very difficult to predict the effect of herbicides on VAM fungi because different results have been obtained with herbicides belonging to the same group of chemicals, or even with the same herbicide. For example, atrazine can increase VAM symbiosis, but in another experiment had no effect, even at high doses.^{4,39} This is probably due to the different experimental conditions (rather than differences in the doses applied or type of VA endophyte) under which the herbicides were used.⁴ The support of culture also influences the action of herbicides. For example, MCPA negatively affected VAM symbiosis when applied to sand-vermiculite, but no effect was observed when it was applied to soil pots.⁴¹ The species or even the cultivar of host plants can also influence the action of the herbicides. Simazine negatively affected VAM colonization and plant growth of citrus and wheat, but not of *Chenopodium quinona*.^{3,43,47} When this herbicide was applied at low doses (0.1 ppm), it inhibited both growth and VA metabolic activity of the fungus in the wheat cultivar 7-Cerros, but had no effect on the wheat cultivar Champlain.⁴³

Recent examinations of VAM symbioses have indicated that VA fungi may improve host resistance to herbicide stress.^{3,38,48} VA mycorrhizal fungi may alleviate the deleterious effects of the herbicides cyanazine, MCPA, and phenmedipham, and even increase the growth of plants treated with chlortoluron when were applied at low or intermediate doses. The effectiveness in improving host resistance varied with different endophytes; this effect seemed to be independent of the capacity of the different endophytes to improve plant growth.⁴¹ However, the beneficial effect of VAM disappeared when the herbicides were applied at higher doses. These results suggest that under agricultural practices, herbicide residues in soil, accumulated from repeated applications, may eliminate the tolerance of VAM plants to herbicides. However, this protective effect cannot be generalized for all herbicides. For example, *G. mosseae* was able to remove atrazine from the soil and transfer it to maize plants, thus increasing the sensitivity of this plant to the herbicide.⁴⁹ This result contradicts observations by other authors (see above).

D. INSECTICIDES AND NEMATICIDES

Few studies have investigated the influence of insecticides and nematicides on VAM. Some of these compounds, such as aldicarb, BHC, diazinon, DBCP, dichloropropene, dimilin, ethoprop, heptachlor, and phorate have been found not to affect VAM symbiosis or to enhance it.⁴ Although a slight decrease in root length colonization of onion treated with aldicarb has been observed,⁵⁰ this nematicide usually did not affect, or even enhanced, VAM symbiosis.^{3,15,44} Aldicarb may have phytotoxic effects on some plants, but VA colonization limits the phytotoxic effect of this nematicide; VA fungi less sensitive than the host plant may alleviate the negative effect of aldicarb.¹⁵

Other insecticides-nematicides such as carbaryl, carbofuran, chlorfenvinphos, DDT, endosulphan, ethoprophos, formothion, malathion, monocrotophos, and parathion may negatively affect the colonization of plant roots when applied at high doses, and fenamiphos and fensulfothion can have a variable effect.^{3,4,17,51-53}

Available data on the physiological and ecological roles of these chemicals are so scarce that it is almost impossible to establish the mode of action of these products on VAM symbiosis.

B. FUNGICIDES

The application of fungicides to field crops to control soil-borne plant diseases is now a common practice. The effects of more than 40 fungicides on VA mycorrhizas have been described.^{2,4,15-17} Bayton, captan, chloranilformethane, chloronitropropane, chloronitride, dichlofuanid, ethirimol, ethylmercuric chloride, folpet, fosetyl-Al, metalaxyl, 2-methoxyethylmercury silicate, PMA, plifenate, prothiocarb, pyrazophos, tridemorph, and triflorine have been found to negatively affect VAM. The other fungicides described had variable effects on VAM. The variability in the mode of action of fungicides on VA mycorrhizas was independent of systemic or nonsystemic properties, or the type of fungicides.^{2,4} Their effects seem to be influenced by the type of fungus, soil, dose of fungicide, and, perhaps, the host plant.

Benomyl, (methyl *N*-1-(butylcarbonyl)-2-benzimidazole carbamate), one of the most extensively studied fungicides, generally depressed VA colonization and spore formation.^{2,4,18-21} Benomyl generally decreased VAM colonization, regardless of the species of fungus colonizing the roots, when applied directly to soil or sprayed onto the surface during the growth period of the plants.^{16,20,24-25} Benomyl has been used to control VAM colonization, both in pot cultures and in the field.^{18,19,25,26}

Benomyl inhibited spore formation and hyphal growth of *Glomus caledonicum* and *G. margarita* on water agar, probably because of the action of the methyl-2-benzimidazole carbamate (MBC), one of its two hydrolysis products; *n*-butyl isocyanate (BIC), the other product, had no observable effect.^{27,28} The ability of *G. caledonicum* spores to germinate after being removed from medium containing benomyl indicates that benomyl, while inhibiting VA hyphal growth, does not kill spores.^{19,27} Benomyl nevertheless did reduce levels of VA colonization, presumably by inhibiting root colonization. This fungicide alters the morphology of the fungus, decreasing its metabolic activity, as confirmed by the rapid decrease in succinate dehydrogenase activity in the internal mycelium developing within roots, and immediately halting the spread of colonization.^{26,29} Benomyl also decreases the rate of plant growth, probably as a consequence of reduced P inflow.^{19,21,25,26} However, the effects of benomyl on growth of VAM plants were not restricted to P uptake, and there are suggestions that some more substantial changes in the physiology of the plants may have been brought about.²⁵

The mechanism of the action of benomyl on VAM formation, however, is not thoroughly understood.¹⁹ Benomyl applied as a seed coat did not affect mycorrhizal colonization, and its symbiotic activity suggested that the influence of fungicides coated onto seeds does not extend far beyond the spermosphere.¹⁶ When applied as a spray, VA colonization was occasionally inhibited. This failure of action was attributed to the difficulty of benomyl in reaching the soil.^{19,25,30} However, the persistence of benomyl in a soil may be related to the pH, organic content, and the adsorption capacity of the soil.^{19,27} On the other hand, benomyl can inhibit extraradical mycelial growth without altering internal colonization.¹⁹ In fact, it has been found that benomyl did not influence VAM colonization once the fungus became established.²² These results indicate that the action of benomyl is more closely related to the inhibition of hyphal development in the rhizosphere than to the development of fungal structures in the roots. When benomyl apparently depressed colonization levels over time, this was probably due to new root growth failing to become infected.¹⁹

Other fungicides, such as fosetyl-Al, significantly increased VA colonization of plant root and favored the growth of fungal structures and their metabolic activity. These parameters increased as the concentration of the fungicide applied increased. The increased growth of mycorrhizal plants treated with the fungicide strongly paralleled increases in percentage colonization by the VA fungus.³¹⁻³⁴ The mechanisms by which fosetyl-Al stimulated VAM colonization is unknown, but they seem to point toward a direct effect of the chemical on the plant, the mycorrhizal fungus, or both.^{33,34} However, some reports indicate that fosetyl-Al had no effect on VAM association.^{35,36} When sprayed onto the leaves of plants grown in the field, the fungicide had no effect on P uptake by established VA mycorrhizal fungi.³⁷

C. HERBICIDES

Herbicides, a group of chemicals used to control weeds, are expected to affect VAM symbiosis because of their toxicity to a wide range of plants, many of them hosts to VAM fungi. Some herbicides, such as atrazine, bromacil, chlorpropham, dichlofopmethyl, diphenamid, diuron, napropamide, phen-

I. INTRODUCTION

The vesicular-arbuscular mycorrhizal (VAM) symbioses are widespread throughout the vegetable kingdom. They benefit the host plant primarily by increasing the capability of the root system to absorb and translocate phosphorus (P) through an extensive network of external hyphae.¹ As the fungi are partly inside and partly outside the host, external factors such as the application of pesticides or the presence of plant pathogenic organisms will affect the development of the symbiosis. Furthermore, the application of pesticides will affect the antagonistic interaction between VAM and plant pathogenic organisms and their subsequent beneficial effect on plant development and growth.

In this chapter the different effects of pesticides and plant pathogens on VAM symbiosis are reviewed.

II. EFFECT OF PESTICIDES ON VA COLONIZATION AND PLANT GROWTH

A. GENERAL BIOCIDES

The effect of several biocides on VAM which may or may not affect VAM colonization and spore germination has been studied. The biocides formalin and, when applied at high doses, sodium azide, dazomet, and metam sodium consistently reduced mycorrhizal colonization. Other biocides such as formalin, methylenebis thiocyanate, vorlex, and, at high doses, dazomet have negative effects on VAM spores. However, 1,3-dichloropropene, ethylene dibromide, vorlex, and mercuran do not affect VAM colonization, and bis-bromocetoxy-2-butene, ethylene dibromide, and sodium azide do not affect spore number.²⁻⁴

The sensitivity of VA mycorrhizal structures varies depending on the biocides used, for example, sodium azide does not affect or may increase spore formation, whereas at high doses sodium azide negatively affects VAM colonization.⁵ However, vorlex affects VAM colonization, but does not affect the formation of spores.⁶ The causes of these differences are unknown.

Most research has been done with methyl bromide. This seems to be the most potent biocide studied and appears to be notably toxic, especially when mixed with chloropicrin, to VAM fungi. Many researchers have used this fumigant to eradicate VAM fungi and other microorganisms from experimental soils.^{2,7} However, most of the seedlings that survived on fumigated plots were mycorrhizal. This was probably a result of low deep penetration of methyl bromide, which may have interfered with the elimination of VAM fungi. These factors can affect the recolonization of these soils by VA fungi and may also contribute to the rapid increase in VA mycorrhizal population after fumigation.^{2,7,8} The population of total propagules may be higher than the population in nonfumigated soil.⁹ Why VAM fungal populations in these cases became larger in fumigated than in nonfumigated soils is not known. However, recolonization of some of the fumigated soils seems not to occur from deep in the soil, but to occur randomly within the soil profile.² No data on the source of propagules involved in the recovery of soils fumigated with methyl bromide are available.⁹

Resistance of VAM propagules to methyl bromide seems to depend on the efficiency of fumigation, which is affected by soil type, dose, and size and type of VAM population.^{2,10} Species of *Gigaspora*, *Acaulospora*, and *Sclerocystis* were more susceptible to fumigation and less able to reinvade fumigated soils than species of *Glomus*.^{9,10} While propagule populations were reduced to below or near detectability by fumigation with methyl bromide, spore populations either were unaffected or slightly reduced.¹⁰ Spores were apparently killed by fumigation, but survived at least several months in ostensibly normal condition.

After fumigation of some soils, plants grew very poorly and became stunted.¹¹ Plant stunting has been attributed in recent years to P deficiency caused by the eradication of mycorrhizal fungi with methyl bromide treatment.¹² Stunted plants lacked VAM fungi and contained low levels of P in their shoots. Stunting can be overcome by either increasing P concentration in the soil or by reinoculating the soil with effective VAM fungi.^{1,13} However, in several fumigated soils P uptake by plants was not enhanced by applications of phosphate, even at high rates.^{8,14} Thus, the improved P nutrition hypothesis does not explain all the effects of VAM on plant growth in soils fumigated with methyl bromide.

INFLUENCE OF PESTICIDES ON VA MYCORRHIZAE

Juan A. Ocampo

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