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Mycorrhiza

Stimulation of vesicular-arbuscular mycorrhiza by fungicides or rhizosphere bacteria

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Abstract. Stimulation of vesicular-arbuscular (VA) mycorrhizal fungi may secure the early establishment of symbiosis and benefit the host plant at an earlier stage of development. The application of *Bacillus mycoides* resulted in particular in the acceleration of early VA mycorrhiza formation. An increase in vigour of the symbiosis could be measured later in terms of increased sporulation of the mycorrhizal fungi after shoot removal. Natural sporulation during later mycorrhizal development was affected by combination of bacteria and just one mycorrhizal isolate. The stimulation of mycorrhizal development was shown to be non-specific with regard to host plant and the isolate of the VAM fungus. However, the effect could not be achieved in all combinations of soil types and host plants. Application of the systemic fungicides triadimefon and pyrazophos promoted VAM formation. Combinations of fungicide and bacterial treatments were not synergistic.

Key words: *Bacillus mycoides* – Accelerated formation – Sporulation – Triadimefon – Pyrazophos

Introduction

Populations of microorganisms in the vesicular-arbuscular mycorrhizal (VAM) rhizosphere vary in their specific composition (Meyer and Linderman 1986), due to variation in growth parameters in the vicinity of symbiotic roots. As already reported briefly (von Alten et al. 1991), there may also be a strong influence of several organisms of the mycorrhizosphere on VAM development. Positive effects may be used to increase VAM formation. The sooner the vesicular arbuscular (VA) mycorrhiza develops, the sooner the host plant will benefit from the symbiosis in the form of increased growth or increased tolerance to stress situations.

Mycorrhizal development and sporulation are in general highly dependent on various biotic and abiotic factors, such as light intensity, temperature, fertilization, substrate and the host genome (Powell and Bagyaraj 1984). In addition, bacteria are known to have beneficial (Bagyaraj 1984) or detrimental (Wilson et al. 1988) effects on mycorrhizal development. However, the majority of experiments so far on combined inoculation of selected bacteria and VAM fungi were aimed at an increase in host growth (Linderman 1988) rather than at the stimulation of VAM development and sporulation. Increased sporulation of VAM isolates may benefit practical plant production on the one hand by improving their competitiveness in soils and on the other hand by improving the quality of inoculum production.

In agriculture, VA mycorrhizae are seldom taken into account, and crop rotation, fertilization, and measures for plant protection (Hayman 1982; Baltruschat and Dehne 1986) may even limit the development of the symbiosis. To utilize the beneficial potential of VA mycorrhiza, the symbiosis must be protected and promoted. This may be achieved by various cultivation practises, e.g. the inoculation of effective isolates of mycorrhizal fungi or combined application of bacteria and VAM fungi. The choice of the fungicides for disease control on VAM host plants may also be of importance. The first description of promoting effects of systemic fungicides on VAM fungi was given by Dehne (1986), and the present report concerns further investigations of this interesting phenomenon in relation to the use of VAM fungi in practice.

Materials and methods

Host plants

Barley (*Hordeum vulgare* L.; cv. 'Gimpel', cv. 'Gerbel'), flax (*Linum usitatissimum* L.), Marygold (*Tagetes erecta* L.; cv. 'Mammut Mum'), tobacco (*Nicotiana tabacum* L.; cv. 'Samsun'), broad bean (*Phaseolus vulgaris* L.; cv. 'Saxa'), cucumber (*Cucumis sativus* L.; cv. 'Mervita'), tomato (*Solanum lycopersicum* L.; cv. 'Haubners Vollendung'), wheat (*Triticum aestivum* L.; cv. 'Kanzler'), onion (*Allium cepa* L.; cv. 'Stuttgarter Riesen'), maize (*Zea mays* L.; cv. 'Saphir').

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Microorganisms

The bacterium *Bacillus mycoides*, and as VAM fungi: three field isolates (species mixtures; isolates no. 510 and 515) and cleaned isolates (one species) of *Glomus etunicatum* (isolate no. 48), *G. mosseae* (isolate no. 114), and *G. intraradices* (isolates no. 18, 20, and 49).

Growth conditions

Experiments were conducted in the greenhouse at 25° C in plastic pots and a photoperiod of 16 h (supplemented with Phillips GSR 102/400 sodium pressure bulbs). Substrates used were either pure sand with a grain diameter of 2 mm, or one of five different soils from the Hannover area. Greenhouse plants were fertilized once per week with 30 ml of a 0.8% or 0.3% solution of 'Wuxal-Normal' (N-P-K = 12-4-6) for dicots and monocots, respectively. For the field experiment with maize, 10-l pots with sand were used for each plant. The drought stress experiment was also conducted outside of the greenhouse using 5-l pots, the water supply to which was controlled by an electronic rain shelter.

Inoculation procedure

Bacteria were grown in a synthetic nutrient medium (Lindemann 1991). VAM inocula were cultivated in expanded clay (Dehne and Backhaus 1986). For inoculation, both microorganisms were applied with the same particles and mixed into the substrate at sowing.

Quantification of VA mycorrhizae

The intensity of mycorrhizal development was measured using a light microscope as the frequency of colonized root pieces. As an additional parameter of vitality, mycorrhizal fungi were allowed to sporulate for 2 weeks after removal of the host shoots. Spore density was quantified according to Land (1991).

Fungicide application

Barley plants were sown in a row in plastic pots so that the soil surface could be covered during foliar application. The volume of fungicide solution applied was 20–30 ml, depending on the growth stage of the plants. Concentrations used were those recommended in practice (Table 1). Controls were treated with distilled water.

Statistical analysis

Values obtained were checked by analysis of variance (ANOVA). Means were analysed in pairs applying the *t*-test, and the Tuckey Test was applied for multiple comparison.

Results

VAM-promoting bacteria and fungicides

Several bacteria isolated from rhizosphere soil were tested for effects on VA mycorrhiza formation. One bacterium which repeatedly gave positive results was an isolate of *B. mycoides*, and this was chosen for the experiments presented here. In reisolation experiments with a streptomycin-resistant mutant of the *B. mycoides* isolate (data not shown), the spore-producing bacterium could easily be reisolated from sand, inoculum particles, and the root surface. There was no accumulation of bacteria in the rhizosphere.

VAM development followed a sigmoid curve in control plants, as well as in plants treated with the bacteria. In flax and barley, which represent plants with fast and slow formation of VA mycorrhiza, respectively, the application of bacteria led to accelerated colonization of the roots (Fig. 1). An earlier initiation of mycorrhizal infection was not observed. When the symbiosis had

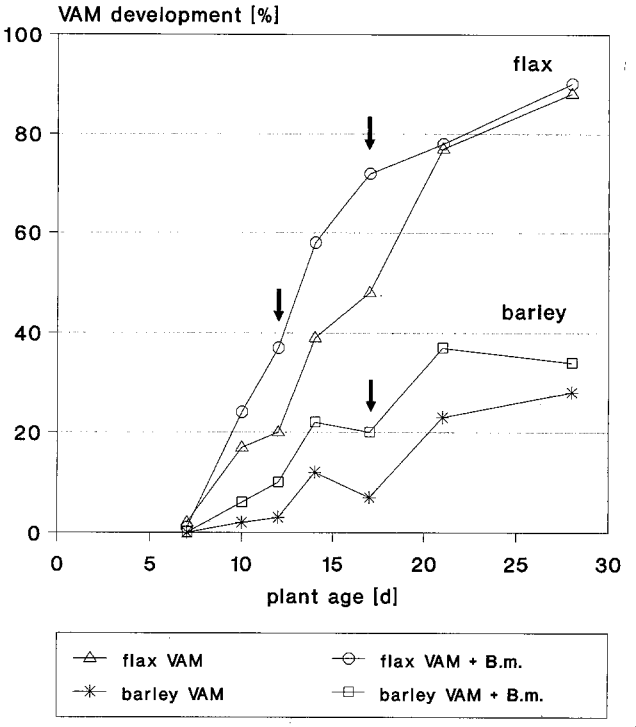

Fig. 1. Effect of *Bacillus mycoides* inoculation on mycorrhizal development (VAM %; isolate 510) in flax and barley. *Arrows* indicate $P \leq 0.05$

Table 1. Fungicides used to influence VAM development

Fungicides	Active agent	Concentration used	
		Product (%)	Active agent (ppm)
Vigil	Diclobutrazol (125 g/l)	0.25	312
Desmel	Propiconazol (250 g/l)	0.125	312
Afugan	Pyrazophos (294 g/l)	0.5	1470
Derosal	Carbendazim (360 g/l)	0.125	450
Sportak	Prochloraz (400 g/l)	0.3	1200
Bayleton	Triadimefon (250 g/kg)	0.125	312
Corbel	Fenpropimorph (750 g/l)	0.25	1875
Saprol	Triforine (190 g/l)	0.25	475
Milgo-E	Ethirimol (280 g/l)	0.25	700

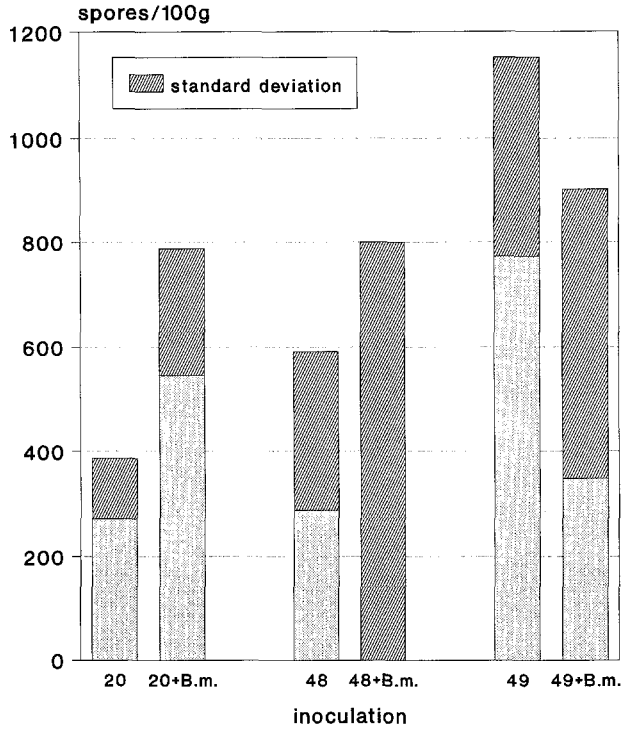

Fig. 2. Effect of *B. mycoides* inoculation on the sporulation of three VAM isolates (20, 48, 49) in maize after 5 months

Table 2. Effect of *Bacillus mycoides* inoculation (B.m.) on mycorrhizal development (isolate 510) after 4 weeks, measured as frequency of colonized root pieces (VAM%) or spore production after shoot removal. * $P \leq 0.05$

Plant	Inoculation	VAM%	Spore production after shoot removal (spores/50 g sand)
Barley ('Gimpel')	VAM	28	81 (100%)
	VAM+B.m.	34	117* (144%)
Flax	VAM	88	366 (100%)
	VAM+B.m.	90	764* (209%)

reached its maximal density, which is fixed by the plant genome and experimental conditions, differences between treated and non-treated plants could no longer be detected.

Quantification of the frequency of colonized root pieces within the root systems is not sufficient to describe the activity and vitality of the symbiosis. To at least partly overcome the lack of parameters measuring these aspects, shoots of 4-week-old host plants were removed and the intensity of sporulation in the following 2 weeks used as a measure of the vigour of the symbiosis. At this time (plant age = 4 weeks) when differences in the frequency of colonized root pieces in the root systems were often no longer apparent, the symbiosis still showed increased vitality under the influence of *B. mycoides* when measured as 'sporulation vigour' after shoot removal (Table 2).

The natural sporulation of the VAM fungi was also affected by the bacterial treatment, although spores were harvested 5 months after introduction of *B. mycoides* into the substrate. However, only one of three fungal isolates showed a significantly altered rate of spore production (Fig. 2).

Further experiments with different combinations of mycorrhizal fungi (Table 3), host plants (Table 4), and soil types (Tables 5, 6) showed that the VAM-promoting activity of *B. mycoides* is a non-specific phenomenon. Nevertheless, in certain combinations of soils and host plants the bacteria failed to accelerate VAM formation.

Systemic fungicides may be useful tools for the manipulation of VAM fungi. Hence, the influence of systemic fungicides on VAM formation was investigated. Nine fungicides were screened for effects on mycorrhizal development after repeated foliar application to barley 21- and 28-day-old plants (Table 7). Two fungicides (Py-

Table 3. Effect of *B. mycoides* inoculation (B.m.) on the development (VAM%) of different VAM isolates in flax. * $P \leq 0.05$

Inoculation	Optimum of VAM enhancement in days after inoculation	VAM%
VAM isolate 48		17
VAM isolate 48+B.m.	21	24*
VAM isolate 114		12
VAM isolate 114+B.m.	28	22*
VAM isolate 510		27
VAM isolate 510+B.m.	14	64*
VAM isolate 515		12
VAM isolate 515+B.m.	14	28*
VAM isolate 18		21
VAM isolate 18+B.m.	24	54*

Table 4. Effect of *B. mycoides* (B.m.) inoculation on the development (VAM%) of VAM isolate 510 in different host plants. * $P \leq 0.05$

Plant	Inoculation	Optimum of VAM enhancement in days after inoculation	VAM%
Linum usitatissimum	VAM		20
	VAM+B.m.	12	37*
Tagetes erecta	VAM		25
	VAM+B.m.	11	44*
Nicotiana tabacum	VAM		27
	VAM+B.m.	14	52*
Phaseolus vulgaris	VAM		24
	VAM+B.m.	11	36*
Cucumis sativus	VAM		23
	VAM+B.m.	11	36*
Solanum lycopersicum	VAM		31
	VAM+B.m.	17	45
Hordeum vulgare	VAM		7
	VAM+B.m.	16	20*
Triticum aestivum	VAM		21
	VAM+B.m.	12	33

Table 5. Effect of *B. mycoides* inoculation (B.m.) on the development (VAM%) of VAM isolate 510 in 14-day-old flax grown in different soil types. * $P \leq 0.05$

Soil type	Inoculation	VAM%
Pelosol	VAM	15
	VAM + B.m.	32*
Black earth	VAM	25
	VAM + B.m.	47*
Para-brown earth	VAM	52
	VAM + B.m.	74*
Brown earth on sand	VAM	24
	VAM + B.m.	19
Para-brown earth on sand	VAM	29
	VAM + B.m.	20

Table 6. Acceleration of development (VAM%; after 52 days) of VAM isolate 510 by *B. mycoides* inoculation of barley ('Gerbel') in two soil types. * $P \leq 0.05$

Soil type	Inoculation	VAM%
Brown earth on sand		
Sterile	VAM	71
	VAM + B.m.	78*
Not sterile	VAM	82
	VAM + B.m.	85
Para-brown earth on sand		
Sterile	VAM	17
	VAM + B.m.	51*
Not sterile	VAM	47
	VAM + B.m.	65*

Table 7. Effect of fungicides on development (VAM%) of VAM isolate 510 in 42-day-old barley plants ('Gimpel') (foliar application to plants aged 21 and 28 days). * $P \leq 0.05$

Fungicide	VAM%	Fungicide	VAM%
None	50	Fenpropimorph	54
Diclobutrazol	46	Triforine	62
Propiconazol	10*	Pyrazophos	70*
Triadimefon	64*	Carbendazim	42
Prochloraz	17*	Ethirimol	62

Table 8. Effect of fungicides applied once or twice on the development (VAM%) of VAM isolate 510 in 17-day-old barley plants ('Gimpel'). * $P \leq 0.05$

Application and plant age	Fungicide	VAM%
—	None	11
Twice	Pyrazophos; 1470 ppm	18*
7th and 11th day	Triadimefon; 312 ppm	18*
Once	Pyrazophos; 1470 ppm	10
7th day	Triadimefon; 312 ppm	19*
	Triadimefon; 31 ppm	9

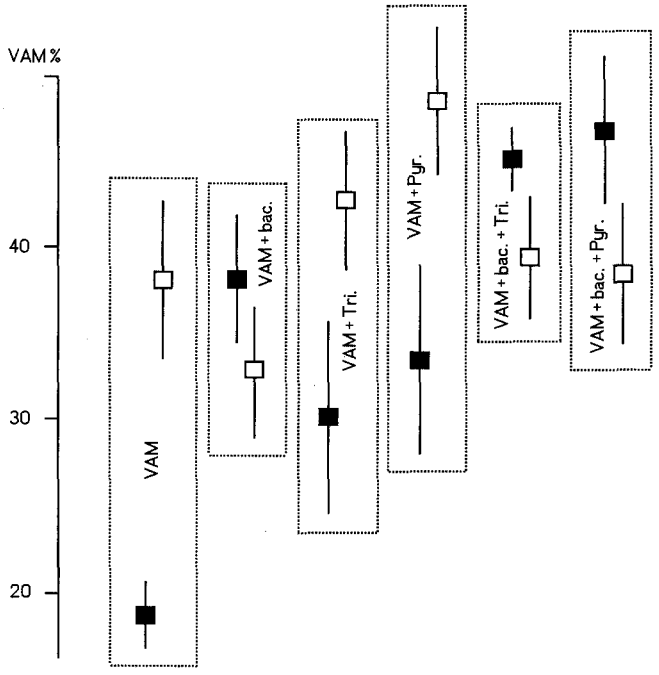

Fig. 3. Effect of combined treatment of barley ('Gerbel') with *B. mycoides* (*bac.*), pyrazophos (*Pyr.*), or triadimefon (*Tri.*) on mycorrhizal development (VAM%) after 18 days (*filled squares*) and 25 days (*open squares*). Standard deviations are indicated

razophos and Triadimefon) were found to increase VA mycorrhizae, and two others were found to have the opposite effect (Propiconazol and Prochloraz). Fungal colonization was even increased when very young plants were sprayed twice after the first leaf had developed completely (at age 7 and 11 days) (Table 8). However, a certain intensity of fungicide treatment was necessary to induce improved VAM development. When applied only once, Pyrazophos was no longer effective. Triadimefon also failed to increase VA mycorrhizae when the effective fungicide concentration was reduced to one-tenth.

Combined applications of bacteria and fungicide failed to show the hoped for synergistic or at least additive effects. In many experiments with barley and cucumber (data not shown) involving *B. mycoides*, other VAM-promoting bacteria (data not shown) and the two fungicides mentioned, the results were disappointing. Figure 3 presents an example with barley.

Effect of VAM promotion on host plants

Plants may benefit from an acceleration of symbiotic development in terms of better growth or better stress tolerance, according to the prevailing conditions. At harvest time, non-treated plants may reach the same density of mycorrhizal structures as treated ones. However, when early spread of the symbiosis in the root system is promoted, the host can benefit earlier and may maintain this advantage for a long time. This is demonstrated in Table 9. No difference in the degree of mycorrhizal colonization at harvest was observed in onion

Table 9. Effect of inoculation of onion with *B. mycoides* (B.m.) and VA mycorrhiza on plant growth and VAM development (VAM%; isolate 510) after 56 days. Numbers with same letters are not different. FW, Fresh weight; DW, dry weight

Inoculation	Shoot		Roots		VAM%
	FW (g)	DW (g)	FW (g)	DW (g)	
None	0.38 a	0.03 a	0.29 a	0.01 a	—
B.m.	0.58 a	0.05 a	0.51 a	0.03 a	—
VAM	7.5 b	0.65 b	2.5 b	0.11 b	95 a
VAM+B.m.	9.3 c	0.84 c	2.5 b	0.12 b	98 a

Table 10. Effect of drought stress on growth and VA mycorrhizal development (VAM%) of barley ('Gerbel') treated with two fungicides. $LSD_{0.05}$, 53.1 g/18.5%

Fungicide	Fenpropimorph				Pyrazophos			
VAM inoculation	+VAM		−VAM		+VAM		−VAM	
Drought stress	Yes	No	Yes	No	Yes	No	Yes	No
VAM%	12	11	0	0	5	27	0	0
Growth [shoot FW (g/pot)]	172	198	151	200	159	201	146	201

plants, and mycorrhizal inoculation increased growth significantly. However, the most pronounced increase in growth of onion was achieved by inoculating the plants with both VAM fungus and bacteria.

Besides growth responses due to better nutrition, increased stress tolerance is often a consequence of VA mycorrhiza formation, due to multiple plant-symbiont interactions. A substance applied to the leaves which has an effect on mycorrhizal development in the root system, may interfere with these plant-symbiont interactions. In the first experiments on this possibility, the interaction of drought stress and pyrazophos treatment of mycorrhizal barley plants was tested. Plants without pyrazophos treatment received fenpropimorph, which had no effects on VA mycorrhizae (Table 7), to control powdery mildew. Drought reduced the growth of non-mycorrhizal plants by about 25%, regardless of the fungicide used (Table 10). This damage was less severe in mycorrhizal plants treated with fenpropimorph. However, in drought-stressed plants, VA-mycorrhiza formation was reduced dramatically by pyrazophos and drought damage was as high as in non-mycorrhizal plants.

Discussion

Interactions of VAM fungi and other parts of the natural soil microflora may result in an altered development of VAM symbiosis (Berthelin and Layval 1982; Azcon-Aguilar and Barea 1985; Meyer and Linderman 1986). The experiments presented here show that introduced microorganisms can be used to manipulate VAM symbiosis, with the aim of promoting mycorrhizal development and increasing symbiotic benefits.

The spread of VAM infection in root systems of plants treated with *B. mycoides* as well as of non-treated plants soon reached an exponential phase, particularly in flax. The development of this exponential phase of colonization depends on a number of different factors. Among these are the inoculum density, or rather the relationship between the amount of mycorrhizal and non-mycorrhizal roots, the number of primary and secondary entry points, the density of the root system and a balanced relationship between root growth and hyphal growth (Mosse et al. 1981; Abbott and Robson 1984).

Since mycorrhizal colonization of roots under the influence of *B. mycoides* did not commence earlier, effective differences in the number of early primary infections are unlikely. It seems more likely that once an infection has established the spread of VA mycorrhizas by runner hyphae and secondary infections is stimulated. However, it can not be excluded that the bacteria stimulate more hyphae from distant inoculum particles to set primary infections in the growing root system during the exponential phase of mycorrhizal colonization. The transient nature of the acceleration of VAM development by application of *B. mycoides* may be explained by limitations of the prolongation of this exponential phase.

The method of bacterial inoculation was to dip the mycorrhizal inoculum (particles of expanded clay) into the bacterial culture before mixing it into the substrate. Thus, there are two possible modes of action: (1) stimulation of chlamydospore germination and term-tube growth via direct interaction with the mycorrhizal inoculum; (2) an indirect effect via the plant, including increased attraction of mycorrhizal hyphae towards the roots and an accelerated spread of symbiosis within the root systems. The fact that the promotion of VAM formation by *B. mycoides* proved to be non-specific with regard to host plant and soil type points to a direct mode of action at the inoculum particles. The non-specificity of the results with different VAM fungi and the two soil types, where there was an effect with the host plant barley but not with flax, points towards an indirect mechanism via the plant.

An evaluation of VA mycorrhizae in terms of the cost-benefit relation of the symbiosis requires not only quantification of colonized root pieces within the root system, but also estimation of the real symbiotically active fungal biomass. This is very difficult using microscopy. Therefore, the intensity of chlamydospore production after removal of the shoots was taken to represent the vigour of the symbiosis. Under natural conditions, chlamydospore production is still in an exponential phase when colonization reaches a constant level (Furlan and Fortin 1973, 1977). The maximum rate of sporulation occurs at the stage of seed ripening of the plant (Hayman 1970; Daft and Nicolson 1972; Saif 1977), but sporulation is induced when the shoot is cut off (Redhead 1975). The active biomass of VAM structures in the colonized part of the root systems is the base from which the mycorrhizal hyphae grow out into the

substrate. After an expansion of this base, more hyphae can produce more spores (Hetrick 1984; Douds and Schenck 1990); this seems to be the case after a *B. mycoides* inoculation. The positive correlation between plant growth and sporulation documented by Baylis (1969), Redhead (1975), and Saif (1977) may not be used to explain the results obtained, since there was no growth promotion due to inoculation at the time of shoot removal.

Natural sporulation, which occurs later in the development of mycorrhizal plants, was increased by *B. mycoides* only with one fungal isolate. That means that applications of the bacteria in the field may alter the VAM population pattern with respect to introduced and indigenous fungi by altering inoculum densities.

It may appear strange at first sight to use fungicides for VAM promotion. However, there have been reports that fungicides have no negative (Jalali and Domsch 1975) and even positive effects (Triadimefon; Dehne 1985) on mycorrhizal development. Input of fungicides into the soil can easily be excluded and transport of fungicide compounds from shoots to roots is very unlikely (Erwin 1973; Jakob and Neumann 1987). Thus, the effects of fungicide treatments on VA mycorrhiza are surely indirect via systemic side effects of the fungicide agents on plant metabolism. Triadimefon is known to have side effects, such as more intense greening of leaves, transient growth depression, decrease in contents of xanthophyll, carotinoids and RNA, postponement of senescence, reduced pigment and nucleic acid metabolism, and depression of gibberellin and sterol synthesis (Buchenauer 1987). It seems reasonable to assume that the plant's quality as a mycorrhizal host is improved by these cytokinin-like effects (Förster et al. 1980). Pyrazophos accelerated VAM formation just as well as Triadimefon, and it too obviously has effects on plant physiology, which are as yet not understood (Buchenauer 1990).

As the VAM-promoting activity of *B. mycoides* or the fungicides is at least partly based on indirect mechanisms via alterations in host plant physiology, there are interactions between these influences and other physiological reactions caused, for example, by environmental stress. As shown by the combined applications of bacteria and fungicides or fungicide and drought stress, in such situations the VAM promotion may vanish or be reversed.

VAM formation always means increased consumption of assimilates by root systems. Thus manipulating VAM development only makes sense when host plants can benefit symbiotically from increased root colonization. Joint inoculation with VAM fungi and *B. mycoides* distinctly promoted the growth of onions. Similar results have been reported from many experiments in which bacteria and VA mycorrhiza had been inoculated together (Barea and Azcon-Aguilar 1982; Bagyaraj 1984; Linderman 1988). *B. mycoides* alone had a negligible effect on plant growth, and thus the growth promotion after combined inoculation can not be explained by synergisms of single growth-promoting effects. Obviously, the benefit of better VAM development in the early growth phases accumulates from day to day and plants can maintain an advantage over a long period.

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