Mycorrhizae in Plant Disease Research

Effect of Soil Fumigants and Fungicides on Vesicular-Arbuscular Fungi

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Mycorrhizal fungi are cosmopolitan, beneficial fungi that are associated with the roots of most crops. Mycorrhizal fungi have been shown to consistently stimulate plant absorption of P, Zn, and Cu, but they also can enhance uptake of K, Ca, Fe, Mg, Mn, and S (15,23,37). Due to improved mineral nutrition, plants normally grow more rapidly and appear healthier than nonmycorrhizal plants, especially on soils of low fertility (4–9,15,18, 23–25,37,47,53,55,61,62).

The use of fungicides and fumigants to control soilborne pathogens is commonplace. Recently, concern has developed among agriculturists about the effects of pesticide usage upon beneficial mycorrhizal fungi. Are the benefits of fungicides and fumigants (increased crop growth via destruction of pathogenic organisms) being diluted because they also destroy mycorrhizal fungi and thereby reduce nutrient uptake by crops? A substantial amount of accurate although fragmented data is now available on the interaction between mycorrhizal fungi and fungicides and fumigants. The purpose of this review is to summarize this information, synthesize it into generalizations, and identify areas in need of further research.

Excellent reviews on the application, efficiency, mode of action, and chemistry of both fumigants (14,40,59) and fungicides (14,26,60) are available. These aspects will be discussed only as they apply to vesicular-arbuscular (VA) mycorrhizal fungi. Pesticide nomenclature is that used by Thompson (59,60).

CROP STUNTING FOLLOWING APPLICATIONS OF FUMIGANTS AND FUNGICIDES

Most soil fumigants stimulate crop growth primarily because of the elimination of soilborne pathogens. However, since the first soil fumigants were used in 1869 there have been consistent reports of stunting following fumigation with many crops including avocado (30), citrus (23,29,31,44,55,61–63), cotton (19,65), peach (24,25), soybean (53), white clover (49), and hardwood tree species (7–9,13,51). Many fumigants have been reported to induce stunting following fumigation, including chloropicrin (19,29,30,44), D-D (27–31), ethylene dibromide (27–31), propylene oxide (29,30), vorlex (55), methyl bromide (13,19,23–25,27,44,51,53,61–63), carbon disulfide (27,29,30), ethylene dichloride (27), and vapam (29,61,62). Symptoms of the stunting syndrome include poor growth, and small, chlorotic leaves that may become necrotic at the edges. Older leaves abscise prematurely. Stems are thin and roots are small but otherwise appear normal. Plants may die but normally remain alive

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in the stunted condition (24,25,29,63,65). Concentrations of P, Cu, and Zn in the plant tissues are frequently reduced to deficiency levels (23–25,29,30,63,65). Concentrations of Ca, Na, Mg, Mn, K, B, Si, Li, Fe, and Al can be increased in affected plants and concentrations of salts in leaf tissues of stunted plants may be increased to injurious levels (23,24,30). The addition of heavy applications of phosphate was found to eliminate the stunting following fumigation (23,29,52,63).

A decrease in the availability of soil elements as a result of fumigation was not the cause of the stunting problem since the availability of most soil nutrients was unchanged by soil fumigations (1,24,28,63). In fact, P, Zn, and Cu, which were deficient in stunted plants, were frequently found at higher concentrations in fumigated soils than in corresponding nonfumigated soils (29). Bromine toxicity is often cited as the cause of stunting following fumigation (31). This could explain why methyl bromide or ethylene dibromide could cause stunting, but it could not explain why other fumigants such as chloropicrin or D-D caused similar symptoms. Furthermore, Tucker and Anderson (63) reported that methyl bromide gas dissipated rapidly after fumigation and stunted plants had not accumulated greater quantities of bromide than nearby healthy plants.

For many years the mysterious stunting agent eluded scientists. In 1963, Martin et al (29) summarized the results of Robinson (52) and others on the stunting-following-fumigation problem and concluded that the stunting was caused by an unidentified substance that was not NO_3, NO_2, NH_4, Mn, Al, Fe, Cl, SO_4, or soluble salts and, although the stunting problem could be corrected with applications of P, soil deficiency of P was not the cause. They found the inhibitory condition to last from a few days to several months and most importantly that mixing untreated and treated soil reduced the duration of toxicity.

The solution to the stunting-following-fumigation problem was suggested by Clark (9) when he showed that mycorrhizal inoculum increased growth of tree seedlings in methyl bromide-fumigated soil. Filer and Toole (13) were also aware of the answer when they indicated that stunting of tree seedlings after fumigation occurred only when accompanied by reductions in the population of VA mycorrhizal fungi. Kleinschmidt and Gerdemann (23) conclusively identified the cause of the stunting following fumigation when they discovered that stunted citrus seedlings in a fumigated nursery lacked mycorrhizal fungi, whereas healthy seedlings were mycorrhizal. They also showed that both methyl bromide and steam could induce stunting of citrus by killing mycorrhizal fungi, while seedlings inoculated with mycorrhizal fungi grew normally. Furthermore, they proved that stunted nonmycorrhizal seedlings were deficient in P, Zn, and Cu while VA mycorrhizal fungi enabled seedlings to absorb adequate amounts of these elements. A mechanism for explaining elevated levels of salts in some stunted plants was postulated by Ratnayake et al (50) when they determined that severe P deficiencies induced by lack of mycorrhizae could destroy the selectivity of the phospholipid membranes in root cortical cells, thereby allowing excessive uptake of salts. Mycorrhizal fungi have been shown to provide resistance to salt damage (18).

There are few documented reports of plant stunting after fungicide applications that can be attributed to destruction of mycorrhizal fungi. Stunting following fungicide applications would normally be attributed to phytotoxicity and such compounds would be abandoned in field screening procedures and therefore would never become commercially available. Soil drenches with the systemic fungicides benomyl and topsin were shown to stunt the growth of onion and strawberry (6). In this experiment, benomyl actually increased growth of nonmycorrhizal onions, thereby indicating that benomyl was reducing growth of mycorrhizal plants by inhibiting mycorrhizal symbiosis and not through phytotoxicity. Bailey and Safir (4) also eliminated phytotoxicity as a cause for stunting which they induced on mycorrhizal soybean with soil drenches of benomyl. They attributed the stunting to reduced effectiveness of the mycorrhizal association. Stunting in both cases was achieved with soil drenches. Since benomyl and topsin are normally sprayed on foliage and are not readily translocated to the roots, there is little danger of widespread inhibition of growth in the field from these fungicides.

EFFECTS OF FUMIGANTS ON VAM FUNGI

The effects of fumigants upon root infection and spore development by VA mycorrhizal fungi are summarized in Table 1. The biocidal fumigants such as chloropicrin, formaldehyde, mylone, methyl bromide, vapam, and vorlex consistently reduced mycorrhizal infection, both in the field and in the greenhouse. Mylone, vapam, and vorlex all decompose into methyl isocyanate which for these fumigants is the active fungicidal compound in soil. A similar effect of these three fumigants on VA mycorrhizae should be expected. Methyl bromide appears to be especially toxic to mycorrhizal fungi and many researchers have used this fumigant to eradicate mycorrhizal fungi from experimental soils.

The nematicidal fumigants DBCP, 1,3-D, and ethylene dibromide apparently do not severely reduce mycorrhizal populations in soil. DBCP and 1,3-D are reported to increase mycorrhizal infection and spore production both in the field and the greenhouse. No information is available on the toxicity of D-D toward mycorrhizal fungi, although it has been reported to cause stunting of citrus in the greenhouse (28,29,31).

FUNGICIDE EFFECTS ON VA MYCORRHIZAL FUNGI

Fungicides are generally far less damaging to mycorrhizal populations than fumigants. They typically delay or reduce VA mycorrhizal infection, but rarely eliminate it altogether.

Nonsystemic fungicides. The effects of nonsystemic fungicides upon VA mycorrhizal fungi are summarized in Table 2. It appears that PCNB, thiram, and botran are consistently toxic to mycorrhizal fungi. Difolatan, euparen, lanstan, and maneb can also be toxic to mycorrhizal fungi. Captan, copper sulphate, terrazole, sodium azide, demosan, and daconil apparently are not greatly harmful to mycorrhizal fungi and may increase mycorrhizal infection or development under certain conditions. The ultimate toxic agent for both maneb and thiram is probably ethylenethiuram disulfide (26), which interferes with a multitude of enzyme systems within cells. These compounds should exhibit similar toxicity toward mycorrhizal fungi. PCNB and botran are similar aromatic fungicides which are specific and affect fungi such as *Botrytis*, *Sclerotinia*, and *Sclerotium*. These compounds appear to affect VA mycorrhizal fungi in a similar manner. Botran is an inhibitor of protein synthesis; however, the mechanism of action for PCNB is not clear (26). PCNB has been shown to damage mycorrhizal fungi so severely that P uptake was inhibited (16). The relative ineffectiveness of sodium azide against VA mycorrhizal fungi is surprising, but Nemec (41) suggests that VA mycorrhizal fungi, like their ectomycorrhizal counterparts, may possess azide-resistant respiration and exposure may actually result in increased growth.

Systemic fungicides. The effects of systemic fungicides upon VA mycorrhizal fungi are summarized in Table 3. Banrot, benomyl, calixin, cela W524, ethirimal, imugan, thiabendazole, topsin, triademifon, and vitavax all appear capable of reducing infection or development of VA mycorrhizal fungi. Pyroxychlor, aliette, terrazole, prothiocarb, and ridomil apparently do little if any damage to mycorrhizal fungi, since they are relatively specific for oomycetes. Benomyl is especially toxic to mycorrhizal fungi and has been shown to stunt onions and strawberries by reducing mycorrhizal infection and ultimately P uptake (6). The fungicidal compound for both benomyl and topsin is the decomposition product, benzimidazole-2-yl carbamate, which inhibits mitosis (26). The fungicidal activity of thiabendazole is also quite similar and these three fungicides should have similar activity toward VA mycorrhizal fungi. The fact that VA mycorrhizal fungi appear to be highly sensitive to benomyl, thiabendazole, topsin, and ethirimol is noteworthy since these fungicides are quite specific for the higher ascomycetes, but are relatively inefficient toward the zygomycetes, with which VA mycorrhizal fungi are generally classified. Cela

W524, imugan, and triademifon probably affect VA mycorrhizal fungi by inhibiting ergosterol synthesis, which is how it affects other fungi (26).

MECHANISMS OF ACTION OF FUNGICIDES AND FUMIGANTS AGAINST VA MYCORRHIZAL FUNGI

The effects of most fumigants and fungicides upon mycorrhizal fungi which are consistent for many plant species can be attributed to the toxic effects of the chemicals which are described above. Because a large proportion of mycorrhizal hyphae are inside roots, it would appear that nonsystemic fungicides can affect VA mycorrhizal fungi primarily by inhibiting spore germination and infection processes and so are probably less damaging to mycorrhizal symbiosis than systemic fungicides. Nonsystemic fungicides may postpone infection, but not eliminate it. Demosan, DBCP, terrazole, and PCNB all prevented germination of *Glomus epigaeus* spores, while only mancozeb did not completely inhibit germination (10). Yet several of these pesticides, demosan, DBCP, and terrazole, have been found to actually increase infection and spore production by mycorrhizal fungi. It is postulated that these fungicides may be fungistatic, but once the mycorrhizal fungus gains entry to the root these chemicals have little effect and may actually increase spread within the root.

The systemic fungicides, as a group, appear more damaging to mycorrhizal symbiosis then nonsystemic fungicides. They can affect spore germination and infection, as well as growth of VA mycorrhizae within the root. Since translocation is primarily upward, systemic fungicides would be most damaging to mycorrhizal fungi when applied as soil drenches. Results published

TABLE 1. Summary of the effects of fumigants upon root infection by or development of chlamydospores of vesicular-arbuscular (VA) mycorrhizal fungi

Fumigant	Host	Effect of fumigant on root infection by VA mycorrhizal fungi	Effect of fumigant on chlamydospore development by VA mycorrhizal fungi	Reference
chloropicrin	cotton	reduced	reduced	Hurlimann (19)
	citrus	reduced	reduced	O'Bannon and Nemec (44)
1,3-D (Telone)	cotton	increased	increased	Bird et al (5)
	citrus	no effect to reduced	...	O'Bannon and Nemec (44)
	citrus	no effect	...	Menge (*unpublished*)
DBCP	cotton	increased	no effect	Bird et al (5)
	peanut	no effect	...	Backman and Clark (3)
	soybean	increased to no effect	increased	Kinloch and Schenck (22)
	grape	...	no effect	Atilano and Van Gundy (2)
	sudangrass	increased to no effect	increased to no effect	Menge et al (34)
	citrus	no effect	reduced to no effect	Nemec and O'Bannon (42)
ethylene dibromide	citrus	no effect	...	O'Bannon and Nemec (44)
	citrus	increased to no effect	reduced to no effect	Nemec and O'Bannon (42)
Formaldehyde (formalin)	wheat	...	reduced	Hayman (17)
	citrus	...	reduced	Nemec (41)
mylone (Dazomet)	corn	reduced	...	Nesheim and Linn (43)
	bean	reduced	...	McEwen et al (32)
	barley & corn	reduced to no effect	reduced to no effect	Ocampo and Hayman (45)
methyl bromide	yellow poplar	reduced	...	Clark (8)
	sweetgum	no effect to reduced	...	Filer and Toole (13)
	tree seedlings	reduced	...	Clark (9)
	tree seedlings	...	reduced	Riffle (51)
	pea	...	no effect	Stewart and Pfleger (57)
	citrus	reduced	...	O'Bannon and Nemec (44)
	sudangrass	reduced	reduced	Menge et al (35)
	citrus	reduced	...	Timmer and Leyden (61)
	citrus	reduced	...	Timmer and Leyden (62)
50% methyl bromide/ 50% chloropicrin	cotton	reduced	...	Wilhelm et al (65)
	cotton	reduced	...	Hurlimann (19)
67% methyl bromide/ 33% chloropicrin	tree seedlings	...	reduced	Riffle (51)
	peach	reduced	...	Lambert et al (24)
75% methyl bromide/ 25% chloropicrin	citrus	reduced	...	Kleinschmidt and Gerdemann (23)
vapam (Metham sodium)	corn	reduced	...	Nesheim and Linn (43)
vapam (sodium N-methyl dithiocarbamate)	peanut	no effect	...	Backman and Clark (5)
vapam	citrus	reduced	...	Timmer and Leyden (61)
	citrus	reduced	reduced to no effect	Nemec and O'Bannon (42)
vorlex (dichloropropene)	corn	reduced	...	Nesheim and Linn (43)
	citrus	reduced	...	Schenck and Tucker (55)
	peanut	no effect	...	Backman and Clark (3)

by Jalali and Domsch (21) provide evidence that systemic fungicides affect mycorrhizal growth inside the root where several systemic fungicides, which were applied as foliar sprays, significantly reduced VA mycorrhizal development. This effect may be due to limited downward translocation of the fungicides or these fungicides may alter plant metabolism in such a way as to inhibit mycorrhizal symbiosis (21). Ratnayake et al (50) have indicated that root exudates may be the factor governing mycorrhizal symbiosis. Pesticides that increase root exudation may increase mycorrhizal infection and pesticides that decrease it may decrease mycorrhizal infection. Schwab and Menge (*unpublished*) showed that herbicides that stimulate root exudation also increase mycorrhizal infection. This may explain why DBCP, demosan, sodium azide, ridomil, and terrazole have been found to stimulate mycorrhizal infection. This may be the only explanation for why foliar application of euparen, a nonsystemic fungicide, significantly reduced mycorrhizal infection (21).

Fungicides and fumigants may affect soil and rhizosphere populations of microorganisms. These microorganisms may interact with germination or infection by VA mycorrhizal fungi. Mosse (36) showed that certain bacteria could significantly increase infection by mycorrhizal fungi. Fumigants and fungicides may also reduce numbers of mycorrhizal hyperparasites or predators (2,10) which could ultimately increase mycorrhizal infection.

It has been suggested (2,5,44,57) that fungicides and fumigants reduce root pathogens that compete with mycorrhizal fungi for root nutrients. The best evidence for this hypothesis is presented by Bird et al (5) who found that DBCP reduced plant parasitic nematode populations and increased mycorrhizal infection. However, Menge et al (34) obtained similar increases in VA mycorrhizal infection with DBCP in autoclaved soil without root pathogens. It is suggested that another hypothesis, perhaps root exudation induced by DBCP, could better explain the increased mycorrhizal infection caused by DBCP.

DOSAGE EFFECTS

The majority of researchers reported rates that were recommended for field use. Tarped, field fumigations with methyl bromide (MB) at rates of 336–560 kg/ha normally provide concentrations in the soil as high as 50,000 ppm, which rapidly dissipate (39, Fig. 1). Toxicity of fumigants is dependent on the concentration and the length of time organisms are exposed (C×T). Menge et al (35) determined the LD^{90} for MB on chlamydospores

TABLE 2. Summary of the effects of non-systemic fungicides upon root infection or development of chlamydospores by vesicular-arbuscular (VA) mycorrhizal fungi

Fumigant	Host	Effect of fungicide on root infection by VA mycorrhizal fungi	Effect of fungicide on chlamydospore development by VA mycorrhizal fungi	Reference
botran (Dicloran)	corn	reduced	···	Nesheim and Linn (43)
	corn	reduced	···	El-Giahmi et al (12)
captan	corn	reduced	···	Nesheim and Linn (43)
	wheat	no effect	no effect	Jalali and Domsch (21)
	bean	no effect to increased	···	Sutton and Sheppard (58)
	corn	no effect to reduced	···	El-Giahmi et al (12)
	onion	no effect	···	DeBertoldi et al (11)
	citrus	no effect	···	Timmer and Leyden (62)
	citrus	no effect to reduced	no effect	Nemec (41)
copper sulfate	pea	···	no effect	Stewart and Pfleger (57)
	citrus	no effect	no effect	Nemec (41)
daconil 2787 (chlorothalonil)	citrus	···	no effect to reduced	Nemec (41)
demosan (chloroneb)	lettuce	increased to reduced	···	Spokes and MacDonald (56)
	citrus	···	no effect	Nemec (41)
difolatan (captafol)	citrus	reduced	no effect to increased	Nemec (41)
euparen (dichlofluanid)	wheat	reduced	reduced	Jalali and Domsch (21)
lanstan	corn	reduced	···	Nesheim and Linn (43)
maneb	wheat	no effect	no effect	Jalali and Domsch (21)
	citrus	···	no effect to reduced	Nemec (41)
PCNB (quintozene)	wheat	reduced	···	Gray and Gerdemann (16)
PCNB (terrachlor)	corn	reduced	···	Nesheim and Linn (43)
PCNB	bean	reduced	···	Sutton and Sheppard (58)
PCNB + terrazole	peanut	···	no effect	Backman and Clark (13)
PCNB	corn	reduced	···	El-Giahmi et al (12)
	wheat & millet	reduced	···	Jalali (20)
	sudangrass	reduced	reduced to no effect	Menge et al (34)
sodium azide	peanut	no effect to reduced	···	Backman and Clark (13)
	soybean	no effect	no effect	Kinloch and Schenck (22)
	citrus	no effect to increased	reduced to no effect	Nemec and O'Bannon (42)
	citrus	no effect to increased	···	Nemec (41)
thiram (arasan)	corn	reduced	···	Nesheim and Linn (43)
	bean	no effect to reduced	···	Sutton and Sheppard (58)
	corn	reduced	···	El-Giahmi et al (12)
	wheat & millet	reduced	···	Jalali (20)

of two mycorrhizal fungi was 12,000 ppm for 6 hr or more (C×T 72,000). Mycorrhizal fungi in soil inoculum were killed when fumigated with 12,000 ppm MB for 7 hr (84,000 C×T) or 6,000 ppm MB for 24 hr (144,000 C×T). Mycorrhizal fungi were apparently capable of surviving 3,000 ppm MB for as long as 48 hr (144,000 C×T). Compared to plant pathogenic soilborne fungi, mycorrhizal fungi are extremely sensitive to MB. They are apparently twice as sensitive to MB as *Phytophthora parasitica* and *P. cinnamomi*, about four times more sensitive to MB than *Verticillium albo-atrum*, and about nine times more sensitive to MB than *Sclerotium rolfsii* (38). Therefore, it would be impractical to reduce rates of MB application to allow mycorrhizal fungi to survive. If VA mycorrhizal fungi survived, soilborne pathogens would survive also. It is concluded that most field fumigations with MB are potentially capable of destroying mycorrhizal fungi in the top meter of soil. Riffle (51) documented reduced populations of VA mycorrhizal fungi after MB fumigations at rates as low as 46 kg/ha.

Although field rates of nematicide fumigants were not harmful to VA mycorrhizal fungi, evidence does exist for increased toxicity of these fumigants to mycorrhizal fungi at high rates (29,44).

Dosage effects with nonsystemic fungicides such as difolatan, captan, demosan, thiram, and botran are not always obvious (12,41,43). This probably results from the inability of these fungicides to alter spread of VA mycorrhizal fungi within the root. Maneb and daconil at doses >11.2 kg/ha are necessary to inhibit VA mycorrhizal fungi. Rates of thiabendazole >18 kg/ha are necessary to reduce VA mycorrhizae, while 2.2–4.5 kg/ha of thiabendazole may increase VA mycorrhizal infection (41). Boatman et al (6) and Bailey and Safir (4) report that increased doses of benomyl do not further reduce VA mycorrhizal infection. It is postulated that the low solubility of benomyl does not allow increased concentrations of this fungicide to build up in the soil solution (6).

SENSITIVITY OF VAM SPECIES TO FUNGICIDES AND FUMIGANTS

Many of the observations of pesticides upon mycorrhizal fungi have taken place in the field and no attempt has been made to

TABLE 3. Summary of the effects of systemic fungicides upon root infections or chlamydospore development by vesicular-arbuscular mycorrhizal (VA) fungi

Fungicide	Host	Effect of fungicide on root infection by VA mycorrhizal fungi	Effect of fungicide on chlamydospore development by VA mycorrhizal fungi	Reference
aliette (efosite Al)	lettuce	no effect to increased	...	Spokes and MacDonald (56)
banrot (terrazole + cercobin methyl)	pea	...	no effect to reduced	Stewart and Pfleger (57)
benomyl	cotton	no effect	...	Hurlimann (19)
	wheat	reduced	no effect	Jalali and Domsch (21)
	bean	reduced	...	Sutton and Sheppard (58)
	onion	reduced	...	DeBertoldi et al (11)
	soybean	reduced	...	Bailey and Safir (4)
	red clover onion strawberry	reduced	...	Boatman et al (6)
	citrus	...	reduced	Nemec (41)
	barley	reduced to no effect	reduced to no effect	Ocampo and Hayman (45)
calixin (tridemorph)	wheat	reduced	reduced	Jalali and Domsch (21)
cela W524 (triforine)	wheat	reduced	reduced	Jalali and Domsch (21)
ethirimol	wheat seed	reduced	...	Jalali and Domsch (21)
imugan (chloraniformethan)	wheat	reduced	reduced	Jalali and Domsch (21)
prothiocarb	...	no effect	...	Paget et al (47)
pyroxychlor	pea	...	no effect to reduced	Stewart and Pfleger (57)
	...	...	no effect	Paget et al (47)
ridomil (metalaxyl)	citrus	increased to no effect	no effect	Nemec (41)
terrazole	cotton	no effect	...	Hurlimann (19)
terrazole (etridiazole)	lettuce	no effect to reduced	...	Spokes and MacDonald (56)
terrazole (ethazole)	sudangrass	increased	increased to no effect	Menge et al (34)
thiabendazole	wheat seed	reduced	...	Jalali and Domsch (21)
	bean	reduced	...	Sutton and Sheppard (58)
	citrus	increased to reduced	no effect to reduced	Nemec (41)
	potato	no effect	reduced	Ocampo and Hayman (45)
topsin (Thiophanate)	wheat	no effect	reduced	Jalali and Domsch (21)
	red clover onion strawberry	reduced	...	Boatman et al (6)
triademifon	wheat	reduced	reduced	Jalali and Domsch (21)
	lettuce	reduced	...	Spokes and MacDonald (56)
vitavax (carboxin)	bean	no effect to reduced	...	Sutton and Sheppard (58)

identify the fungal symbiont involved. Variation in effects of pesticides upon mycorrhizal fungi can be attributed to the VA mycorrhizal species involved. To date, effects of fungicides and fumigants have been tested on only six of the more than 40 known species of VA mycorrhizal fungi. The fungi tested are all closely related *Glomus* spp.—*G. etunicatus*, *G. mosseae*, *G. fasciculatus*, *G. macrocarpus*, *G. microcarpus*, and *G. constrictus*. The effect of pesticides on the important VA mycorrhizal genera *Sclerocystis*, *Gigaspora*, and *Acaulospora* are unknown. The effect of fungicides and fumigants upon the VA mycorrhizal species tested so far seems remarkably similar. Menge et al (35) showed that spore germination of *G. fasciculatus* and *G. constrictus* reacted similarly to MB. There is evidence that some species are more sensitive to some fungicides than others. Spokes and MacDonald (56) showed that triademifon, terrazole, and demosan did not affect infection by *G. fasciculatus* after 12 wk. Infection by *G. mosseae*, on the other hand, was reduced to two-thirds of the control by these fungicides. Triademifon reduced infection by *G. microcarpus* by one-half, demosan increased infection by *G. microcarpus* almost threefold, while terrazole had no effect. O'Bannon and Nemec (44) indicated that *G. mosseae* was inhibited by 168 L/ha of 1,3-D while *G. fasciculatus* was not.

REINVASION OF FUMIGATED SOILS

Evidence indicates that most field fumigations are capable of eliminating VA mycorrhizal fungi from the soil. However, crop stunting does not occur on the majority of fumigated sites; instead, growth of crops is usually stimulated by fumigation. How can this apparent anomaly be rationalized? A careful look at data from MB fumigations (Table 1), many of which are carried out under optimum conditions, indicates that VA mycorrhizal populations are not always reduced by MB (13,22,54,55). Rarely if ever are fungi completely eliminated by fumigants, as evidenced by the characteristic patches of healthy plants scattered among the stunted ones in fumigated fields. Many factors affect the efficiency of fumigations, such as temperature, moisture, soil texture, tarping, and organic matter (40). It is very difficult to destroy 100% of any microorganism, especially one as abundant as VA mycorrhizal fungi (35). Much higher doses of fumigant are required to kill fungi when they are embedded in organic matter and most VA mycorrhizal fungi will be embedded in root material unless the field has been fallow for some time. Some mycorrhizal inoculum survived fumigation with MB at 12,000 ppm for as long as 16 hr, roughly 2.3 times the dose required to kill the inoculum of most VA mycorrhizal fungi (35). Hayman (17) indicated that survival of mycorrhizal fungi improved after the second and third fumigation, indicating that populations resistant to fumigation were being selected.

In California, VA mycorrhizal populations were monitored before, and for 13 mo after, MB fumigations by taking 500-g soil samples at 23, 46, 91, and 137 cm depths from four locations within each fumigated area (Fig. 1). These samples were potted, planted with sudangrass, incubated in the greenhouse, and rated for VA mycorrhizal infection after 3 1/2 mo. The effectiveness of the fumigations was also monitored by measuring the concentrations of MB after fumigation at various depths using the methods of Munnecke et al (39). All sites were replanted, disked, fertilized, and

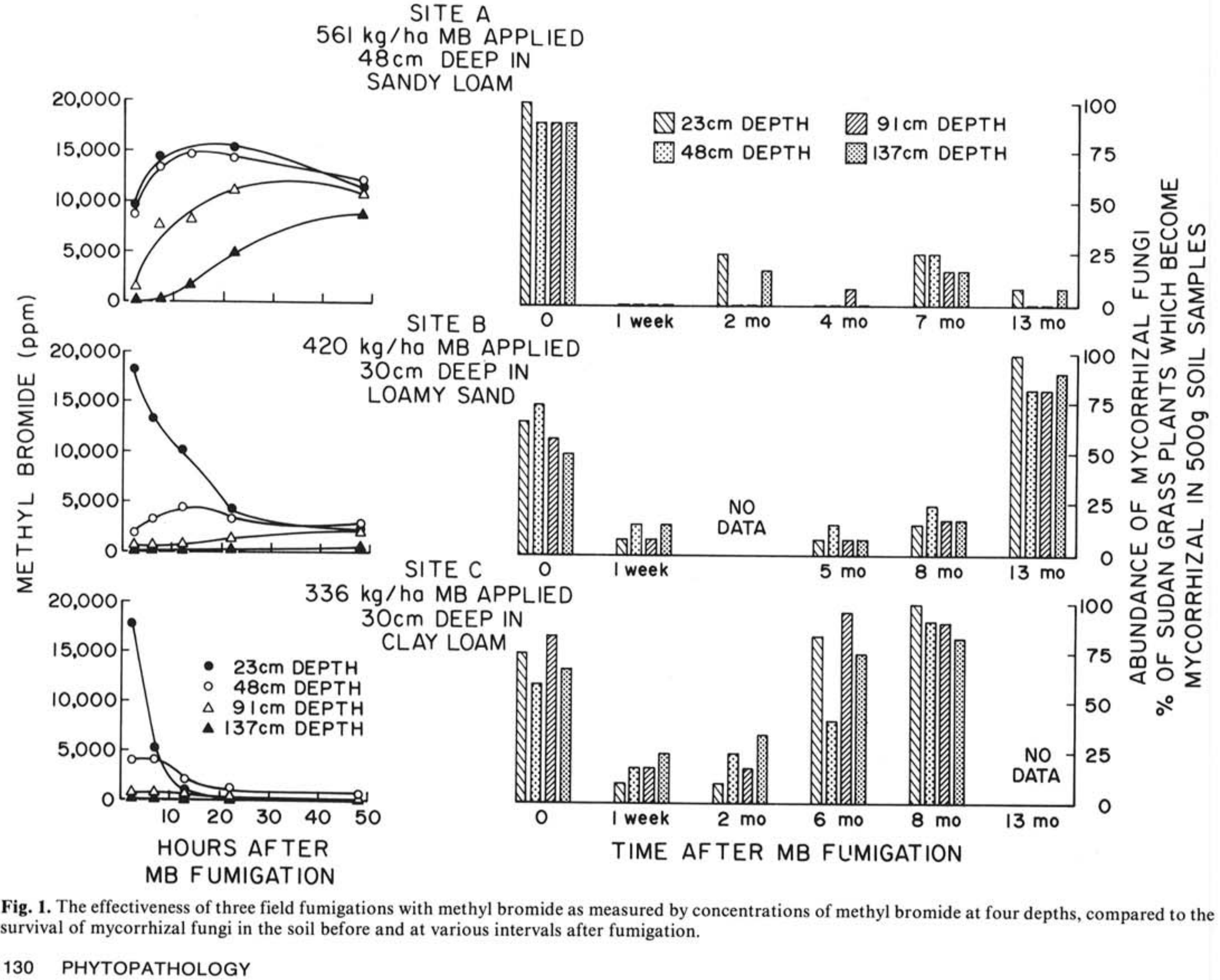

Fig. 1. The effectiveness of three field fumigations with methyl bromide as measured by concentrations of methyl bromide at four depths, compared to the survival of mycorrhizal fungi in the soil before and at various intervals after fumigation.

treated as normal agricultural fields following fumigation. Results are shown in Fig. 1. Dosage responses of VA mycorrhizal fungi reported by Menge et al (35) indicate that the MB fumigation at site A was excellent and that mycorrhizal fungi should have been killed to a depth of 137 cm. The fumigation at site B was less than adequate, probably due to poor tarping, but mycorrhizal fungi should have been eliminated to a depth of 23 cm. At site C, the fumigation was poor because of heavy soil and excess moisture, and mycorrhizal fungi should have survived at all depths. All the MB fumigations severely reduced populations of mycorrhizal fungi but did not eliminate them. Mycorrhizal populations reached prefumigation levels in the poorly fumigated site C within 6 mo. At site B, where fumigation was better, mycorrhizal populations were restored after 13 mo. At site A, where the fumigation was excellent, mycorrhizal populations were still severely reduced after 13 mo. Recolonization of the fumigated sites did not occur either from the soil surface or from deep in the soil but occurred randomly within the soil profile. It appears that recolonization of fumigated sites is correlated strongly with the efficiency of fumigation and that mycorrhizal inoculum that "escapes" fumigation is largely responsible for recolonization.

Reinvasion must also contribute to the rapid increase in VA mycorrhizal populations after fumigation (55). At site A the mycorrhizal population appeared to be eliminated after 1 wk, but 2 mo later, before any crops had been planted or any weeds invaded the site, mycorrhizal fungi were evident. This was observed at several other sites. It is well established that VA mycorrhizal fungi can be spread by earthworms, insects, and small mammals (33). However, VA mycorrhizal inoculum deposited upon the soil surface would not survive long and much of the hypogeal animal and insect fauna is also destroyed by fumigation. Therefore, rapid dissemination of massive amounts of VA mycorrhizal inoculum for long distances into fumigated fields is unlikely. Under desert conditions, a 1-m barrier strip of fallow soil is enough to prevent mycorrhizal infestation of control plots from nearby mycorrhizal plants. Recent evidence (64) indicates that mycorrhizal fungi are capable of limited independent spread in soil, probably via germination, growth, and the formation of secondary spores. It is suggested that this spread may be rudimentary saprophytic growth from an organic base. Ocampo and Hayman (46) support this conclusion; they observed an increase in infectivity in fallow soil kept in the greenhouse for 12 wk after infestation. This type of independent spread may explain the apparent increase in VA mycorrhizal inoculum, which occurs almost immediately after fumigation.

It frequently appears that mycorrhizal infections are more vigorous and abundant in fumigated or sterilized soils than in unsterile soils (48). Fumigations may be reducing hyperparasites, predators, or competing plant parasites and thereby encouraging rapid reproduction of VA mycorrhizal fungi. At any rate, escapes from fumigation, subsequent saprophytic spread, reinvasion, and increased development of VA mycorrhizal fungi in fumigated soil may well explain why plant stunting following fumigation is not a universal phenomenon.

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