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Arbuscular Mycorrhizal Response to Adverse Soil Conditions

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INTRODUCTION

Adverse conditions are a pervasive feature in both natural as well as agronomic soils. The soil environment is constantly changing with regard to moisture, temperature and nutrition. In addition, soil properties such as fertility, pH and aeration are often changed to improve crop yields. Soils have been unintentionally contaminated as a result of accidents that occur during agronomic operations or intentionally contaminated in mining or manufacturing operations by disposal of chemicals that are toxic to plants and micro-organisms. Mycorrhizal associations in terrestrial ecosystems influence organic and inorganic nutrient relationships, water relations and carbon cycling in plants. Relatively little is known about factors that control the vigour and extent of mycorrhization. This lack of understanding arises in large part from the difficulty of studying the intact association, which is a functionally and anatomically distinct structure comprising two biologically different organisms, e.g., plants and arbuscular mycorrhizae (AM) fungi. The formation and function of mycorrhizal relationships are affected by edaphic conditions such as soil composition, moisture, temperature, pH, cation exchange capacity. They are also affected by anthropogenic stressers such as heavy metals, pesticides and soil compaction.

An organism's response to stress may involve interactions among various avoidance and tolerance mechanisms (Taylor, 1978; Tingey and Taylor, 1982; Tingey and Anderson, 1991). Stress avoidance mechanisms influence the amount and rate at which stress will reach the target site in the plant. Stress tolerance is defined as resistance via an ability "to come to thermodynamic equilibrium to the stress" without being killed (Levitt, 1980). In this chapter, we shall review the effects of a number of soil-associated stressers, including soil moisture, temperature, pH, heavy metals, agricultural practices and pesticides on AM development and function and host plant tolerance to these stresses. Several publications have reviewed the impact of various stresses on plant-mycorrhizal interactions (Anderson and Rygiewicz, 1991; Read, 1991; Van Duin et al., 1991; Sylvia and Williams, 1992), which provide additional information on this subject.

NATURAL PRODUCED STRESSERS

Soils rarely provide ideal conditions for growth and survival of plants and soil micro-organisms. Since soil conditions are constantly changing, the soil environment may favor AM development and function at one point in time, and inhibit it at another. The influence of moisture and temperature are examples of these effects. In the section below, changes in mycorrhizal formation and function in plants experiencing extremes in water, temperature, pH and inorganic nutrient availability will be reviewed. Collectively, many studies show that natural and anthropogenic factors impact carbon allocation patterns in both mycorrhizal and non-mycorrhizal plants by a variety of mechanisms.

A. Water

1. Moisture Deficit

Plant response to AM colonization may affect the host plant function and productivity under both high and low moisture conditions. Many of the studies described below have been done in the greenhouse and not in field conditions, so responses under natural conditions are not fully known. In growth chamber studies, Bryla and Duniway (1997a & b) found that plant moisture deficits of—1.5-2.0 Mpa did not affect mycorrhizal colonization or phosphorus uptake of wheat (*Tritium aestivum* L.) plants. In greenhouse studies, Subramanian and Charest (1995) and Schellenbaum et al., (1998) found that drought stressed maize not infected with *Glomus mosseae* (Nicol and Gerd.) or *Glomus intradices* (Schenck and Smith 1982) had higher concentrations of glucose, fructose and total amino acids in

leaves and roots than non-mycorrhizal plants. The AM symbiosis also increased the biomass of two native forage species [(*Baptisia australis* (L.) R. Br. and *Liatris aspera* Michx.)], i.e., greater biomass for mycorrhizal plants, regardless of added levels of fertilizer, compared with nonmycorrhizal plants (Zajicek et al., 1987). However, Simpson and Daft (1990) examined six AM fungal inocula of the genera *Acaulospora* and *Glomus* and found little influence of AM fungi on growth of either corn (*Zea mays* L. cv Drocan PO1) or sorghum (*Sorghum bicolor* L. cv CSH5); withholding water reduced plant growth similarly between the two AM treatments. Colonization levels were increased by drought, while spore production was reduced with regard to both the total number of spores produced and spores per gram of plant weight for most inocula. Sylvia et al., (1993a) conducted field studies to examine the effects of AM on drought-stressed *Z. mays*. The proportional response of the inoculated plants to drought increased with increased moisture deficit. This occurred because grain yield and total above-ground biomass responded positively and similarly to irrigation for both mycorrhizal and non-mycorrhizal plants. The relative beneficial contribution of AM inoculation increased with increasing plant moisture deficit.

The AM symbiosis may alleviate plant responses to moderate moisture deficit by several mechanisms, including increased water uptake due to extraction of water in the soil by hyphae (Augé et al., 1992; Davies et al., 1992), altered hormonal levels causing changes in stomatal conductance (Drüge and Schönbeck, 1992), increased turgor by lowering leaf osmotic potential (Davies et al., 1993), improved nutrition of the host (Johnson and Hummel 1985), and improved plant recovery after drought through improved maintenance of the soil-root continuum (Reid, 1979; Sweatt and Davies, 1984). Some research has shown that drought response of AM plants can be independent of plant nutrition, i.e., phosphorus (Bethlenfalvay et al.; 1988, Peña et al.; 1988, Sanchez-Díaz et al., 1990; Henderson and Davies, 1990, Davies et al., 1993). Goicoechea et al., (1995) suggested the importance of AM symbiosis in maintaining cytokinin levels under drought. When alfalfa (*Medicago sativa* cv Aragón) plants were grown in pots in the greenhouse and subjected to a cyclical drought, mycorrhizal-inoculated plants, which had lower moisture deficits, maintained higher cytokinin levels compared with non-mycorrhizal plants having higher moisture deficits. Mycorrhizal plants also had delayed leaf senescence and stimulated stem production. The authors suggest that different drought responses of the two types of plants were mediated by leaf cytokinin concentrations.

2. Flooding

Compared with the amount of work done on moderate moisture deficit, less research has been done on excessive amounts of water (Keeley 1980; Hartmond et al., 1987). The AM symbiosis has been found in aquatic and wetland plants (Read et al., 1976; Sondergaard and Laeggaard, 1977; Bagyaraj et al., 1979; Chaubal et al., 1982; Tanner and Clayton 1985; Ho, 1987; Dhillion and Ampornpan, 1992). Arbuscular-mycorrhizal colonization has not been found in aquatic macrophytes in the families Cyperaceae and Jancaceae (Kahn 1974; Harley and Smith, 1983; Allen, 1991), but only as mycelial colonization in the rhizosphere and infrequently as deposits in root epidermal cells (Powell, 1975). Lodge (1989), using plants grown in greenhouse, found higher rates of colonization in moist soil as compared with the rates found in very dry or flooded soils. Wetzel and van der Valk (1996) measured AM fungal colonization for 19 plant species growing in several vegetation zones in six wetlands. Each of the six wetlands could be assigned into one of two groups based on organic matter and phosphorus contents, soil pH, and soil salinity. Using principal component analysis, only two environmental factors were significant: location i.e., differences between the two groups of sites for soil pH, phosphorus, specific conductance and season and, vegetation zone i.e., low prairie, wet meadow, shallow emergent. They did multiple regression analyses to evaluate the significance of environmental factors and AM colonization. Their analyses indicated that host plant species, soil phosphorus, and soil pH influenced AM fungal colonization. Many of these observations may be explained by soil redox potential. The numbers of mycorrhizal spores in wetland soils has been positively correlated to redox potential (Kahn, 1993b). Spores were abundant in upland terrestrial soils, moderately abundant to rare in wetland soils and rare to absent in water (Kahn, 1993a and c). Spore germination was found to be inhibited at low O_2 concentration, germination returned to previous percentages when O_2 concentrations were returned to normal (Le Tacon et al., 1983). As with spore germination, Kahn (1993b) found a correlation between mycorrhizal infection and soil redox potential. Mycorrhizal formation was less frequent on tree roots in reducing environments of flooded soils (E_h # 150 mV) than in more aerobic soils (E_h # 300 mV).

Mycorrhizal colonization of the aquatic plant *Vallisneria americana* (Michx.) was found to enhance ^{33}P uptake. In freshwater ecosystems, plants release O_2 into the surrounding rhizosphere which can contribute to reduced P availability. Oxygen release into anoxic soils will combine with iron to form a Fe-OH sheath surrounding the root, which will adsorb phosphate (Janes and Carpenter, 1986). The Fe-OH sheath around roots is a common characteristic of plants growing in anoxic soils (St. Cyr et al., 1993). A more thorough review concerning mycorrhizal formation

and function in wetland ecosystems is found in Kahn and Belik (1995), who provide additional information on this subject. Even though AM fungi are thought to play a critical role in nutrient accumulation and therefore function of wetland and aquatic ecosystems (Tanner and Clayton, 1985; Wigland and Stevenson, 1997), this area of ecological research has received little attention.

Mycorrhizal associations seem to help a plant avoid drought effects. When plants are experiencing moderate moisture deficits, they can still photosynthesize and will allocate an increased amount of carbon to roots and mycorrhizae, hyphal strands of the mycorrhizal fungi will then exploit a greater volume of soil than roots alone, obtaining more water. When plants are experiencing severe moisture deficits, photosynthesis is impaired and less carbon is allocated to roots, therefore mycorrhizal associations and water uptake decrease. Similar responses seem to occur in flooded soils. When flooding is intermittent and the soil moist with a high redox (E_h # 300 mV), plants are mycorrhizal. However, when flooding is continuous and redox is low (E_h # 150 mV), mycorrhizal associations are less likely to form.

B. Temperature

Spores of AM fungi differ in optimum germination temperatures (Saif, 1983; Matsubara and Harada, 1996). Soil temperature alongwith moisture will exert a major influence on mycorrhizal colonization of plants (Braunberger et al., 1997). The influence of temperature on AM fungi is variable, it may be affected by the fungal host-species combination, temperature range for germination of the AM fungi, optimal temperature range for photosynthesis of a host plant, and the developmental stage of the plant.

At constant temperatures, mycorrhiza colonization of asparagus (*Asparagus officinalis* L.) was highest with *Glomus etunicatum* and *Glomus margarita* (Matsubara and Harada, 1996) at 25°C and 25-30°C, respectively. Maximum arbuscular development in soybean [*Glycine max* (L.) Merr.] roots occurred at 30°C with *Endogone gigantea* Nicol. and Gerd., while maximum mycelial development of roots occurred at 28° to 34°C; maximum sporulation and vesicle development occurred at 35°C (Schenck and Schroder, 1974). The efficacy of mycorrhizae at soil temperatures ranging from 18° to 41°C was determined by Schenck and Smith (1982), who found maximum colonization, sporulation, and growth enhancement in soybean at 30°C. Responses were related to the various combinations of soil temperatures and AM fungal species. Infected root length and number of vesicles increased as temperature increased from 20° to 30°C in *Eupatorium odoratum* L. inoculated with *Glomus macrocarpum*, arbuscular development however decreased above 25°C (Saif, 1983).

Furlan and Fortin (1973) found that AM fungi increased growth of onion plants at high temperatures, but at lower temperatures such as 16°C day and 11°C night, inoculated plants grew less than non-inoculated plants. Hayman (1974) found that at 14°C dry matter production of onions inoculated with *Endogone* spores was less than non-inoculated plants when light intensities were reduced; above 14°C, inoculation increased growth of onion. Maximum shoot growth of mycorrhizal cotton (*Gossypium hirsutum* L.) was at 30°C when plants were inoculated with *Gigaspora calospora* and *Glomus intraradices* (Schenck and Smith, 1982). However, maximum growth was at 36°C when plants were inoculated with *G. ambisporum* (Schenck and Smith, 1982). In ash (*Fraxinus pennsylvanica*), Anderson et al., (1987) found greater relative growth rate of leaf area in AM seedlings compared with rates for non-mycorrhizal seedlings at 7.5 and 11.5°C, similar rates at 15.5°C, and greater rates in non-mycorrhizal seedlings at 20°C. Paradis et al., (1995) found that mycorrhizal wheat plants had higher concentrations of chlorophyll and non-reducing sugars than nonmycorrhizal plants at 5 but not at 25°C.

Zhang et al., (1995) examined sub-optimal root zone temperatures and the development of the soybean-AM [*G. versiforme* (Karsten) Berch]-nitrogen fixing (*Bradyrhizobium japonicum*) tripartite symbiosis. Plants were harvested at four growth stages and optimal root zone temperature for colonization of *G. versiforme* was 21-22°C: above and below this temperature, the colonization was inhibited. The optimal temperature of 25-30°C for the AM fungus was not necessarily optimal for nodulation and N_2 fixation (Zhang et al., 1995). The AM fungus negatively affected nodule numbers at lower temperatures. However, the influence was positive at higher temperature. The smaller number of nodules at the lower temperatures was offset by increased specific nodule mass, the endophyte effectively stimulated N_2 fixation at the lower root zone temperatures. The authors concluded that temperature effects are related to photosynthesis and transpiration rates at the various root zone temperatures with more intense competition for photosynthate between the AM fungus and the dinitrogen fixing bacterium occurring at lower root zone temperatures.

The influence of temperature on AM formation is variable and optimum appears to be between 18° and 40°C with most fungal-host species combinations exhibiting an optimum near 30°C. Optimal temperature ranges are dependent on germination temperature of the AM fungi and the optimal temperature of host plant photosynthesis and carbon flow to roots.

C. pH

The response of AM fungi to soil pH is highly variable. Some AM fungi did poorly in low-pH soils, while others performed poorly after acid-

soils were limed (Mosse, 1972a, 1972b). In other studies, AM fungi improved plant productivity in acid soils that were limed (Davis et al. 1983). In yet other acid soils, an AM fungal effect was found to occur without the need of increased pH (Guzman-Plazola et al., 1988; Weissenhorn and Leyval, 1996).

The response of AM-inoculated plants to pH has been studied for some very practical reasons including potential negative effects of the hydrogen ion activity on plant productivity via direct effects on the endophyte and host plant physiology and indirect effects via changes in soil processes, e.g., heavy metal and base cation availability (Habte and Soedarjo, 1996).

AM fungi play an important role in improving plant productivity by enhancing the uptake of nutrients, particularly phosphorus (Smith and Read, 1997). The influence of the AM symbiosis in nutrient absorption depends on the uptake capabilities of the host and the endophyte, the extent of colonization of the root and surrounding soil, and factors affecting the formation and reproduction of the endophyte symbiosis (Foy, 1983; Wang et al., 1985; Habte, 1995). The hydrogen ion activity can affect most, if not all, of these characteristics. For example, availability of P in soil is low at all pH values because P reacts with soil constituents forming insoluble compounds. In general, mechanisms to absorb cations (e.g., NH_4^+, Johansen et al., 1992, 1993a, 1993b; Frey and Schuepp, 1993) and anions (e.g. NO_3^-, Tobar et al., 1994; Bago et al., 1996) by AM fungi appear to be similar to those of other organisms. Some workers have suggested that AM fungi tolerate adverse external pH conditions by modifying the pH of the rhizosphere during the uptake process (Tinker, 1975; Pacovsky, 1986).

The effect of soil pH on AM fungi and AM-inoculated plants was summarized by Sylvia and Williams (1992), who concluded that some AM fungi do not readily adapt to soils with pH unlike that of the soil of origin, and that pH constraints AM establishment. Studies done to help formulate these conclusions involved direct liming of soils (Kucey and Diab, 1984; Newbould and Rangeley, 1984), analyses of AM characteristics across diverse soil types (Skipper and Smith, 1979; Menge et al., 1982; Sylvia et al., 1993b), and varying soil management treatments that involve physical modification or fertilization e.g., organic amendments (Soedarjo and Habte, 1993).

Sylvia and Williams (1992) indicate that it is not clear if AM fungi offer any protection to host plants against detrimental effects of adverse pH conditions. Klironomos (1995) speculated that AM fungi may protect acid-sensitive sugar maple (*Acer saccharum*) in conditions which otherwise would be detrimental. He examined propagule levels and colonization of *A. saccharum* in forests located in southern Ontario on three soil types

(brunisols, luvisols, and podzols). The more acidic, organically-enriched and moist podzolic soils with humus are considered less favourable for AM fungi and generally support ectomycorrhizal associations, brunisols and luvisols are considered more favourable for AM fungi. In luvisolic soils, colonization levels were similar, and spore densities were lower compared with values found for brunisols. Patterns were nearly opposite for roots in podzolic soils where low occurrence of arbuscules, high levels of hyphal coils and vesicles, and much higher spore densities prevailed. Other studies indicate that AM fungi characteristically found in some podzolic soils (Klironomos, 1995) may be indicative of stress (Spkito et al., 1978; Duckmanton and Widden, 1994). These results indicate that AM fungi have the capability to tolerate low pH conditions.

The response of AM fungi to soil pH seems to be dependent primarily on the AM fungal species. Some fungal species readily form AM associations with host plants growing in low-pH soils, while others form AM associations with host plants growing only in higher pH soils. The question posed by Sylvia and Williams (1992) concerning the adaptability of AM fungi to soil conditions unlike those of the soil of origin, is only partially answered. An experiment utilizing a series of reciprocal soil replacements among stands such as those studied by Klironomos (1995) would contribute to answering this question.

D. Nutrients

AM associations enhance plant acquisition of nutrients by increasing the effective surface area of the root system. Mycorrhizae are especially important for plant survival and growth when the soil has low concentrations of plant available nutrients, especially phosphorus. Mycorrhizal roots are able to obtain more nutrients from deficient soils than roots that are non-mycorrhizal because hyphal strands exploit a greater volume of soil than roots alone. Nye and Tinker (1977) showed that the concentration of any immobile element in a soil will follow the laws of physics and be taken up by an absorbing surface. If its rate of absorption exceeds it diffusion rate or the rate at which it moves toward the absorbing surface (fungus or root), the concentration near the absorbing surface will decrease. The concentration of the element in the soil will continue to decrease until the ratio of uptake is equaled by the rate of replacement at the absorbing surface (root or hyphae). A deficiency zone will soon develop around the absorbing surface. At this point, the rate of element uptake increases because the rate of uptake is entirely dependent on the rate at which the element moves (diffuses) through the soil.

Smith and Read (1997) have postulated four possible mechanisms for the increased efficiency of nutrient uptake by mycorrhizal roots:

1. Growth of extraradical hyphae of mycorrhizal fungi by growing into soil not colonized by roots can increase absorption of more nutrients from the soil solution and translocate them to roots. This occurs because the hyphae of mycorrhizal fungi serve to exploit a larger volume of soil outside the element deficiency zone and translocate absorbed elements to the root (Harley 1989). Sanders and Tinker (1971) showed that the translocation of elements (especially immobile elements) in the hyphae of AM fungi was large enough to accommodate the rate of inflow. Hyphae of mycorrhizal fungi also develop deficiency zones about themselves. However, the provision of a new absorbing surface by growth of the hyphae is much less expensive in carbon cost to the plant than growth of a root.
2. Hyphae are more effective than roots at competing with free living micro-organisms for plant-available nutrients.
3. Hyphae may have a higher affinity for nutrients than roots, leading to more effective absorption from soils with low nutrient concentrations (Cress et al., 1979).
4. Mycorrhizal roots can use those sources of nutrients that are not available to roots. This could involve an increased rate of nutrient solubilization of insoluble nutrients, production of organic acids that act as chelating agents, and production of enzymes that can degrade soil organic materials, mineralizing nutrients and translocating them to roots.

Most AM research has focused on host responses of crop plants, rather than natural ecosystems. Studies have shown that AM will influence plant competition, plant demographics, community structure and plant succession (Allen, 1991; Read, 1991; Goldberg and Barton, 1992; Gange et al., 1993; Hartnett et al., 1994; Wilson and Hartnett, 1997). In tall grass prairie ecosystems, warm season grasses are more dependent than cool season grasses on mycorrhizal symbiosis (Hetrick et al., 1988; Hetrick et al., 1990; Wilson and Hartnett, 1997). There is also considerable variation in mycorrhizal formation and function throughout the life of the plant (e.g., establishment, vegetative growth, flowering and seed production) (Wilson and Hartnett, 1997). Since there is normally a great deal of plant diversity in natural ecosystems, the presence or absence of AM fungi in soils can change the competitive balance between obligately mycorrhizal dependent, facultatively dependent and nondependent species and therefore composition and productivity of the ecosystem.

The response of AM plants grown under complete-nutrient regimens was characterized by a multi-phased phenology where changes in gross plant morphology between inoculation treatments did not become ap-

parent until the second growing season (Douds and Chaney, 1986). At that time, differences in mycorrhizal development caused by different nutrient treatments appeared as a difference in mycorrhizal colonization levels, which increased for low-nutrient seedlings and decreased in high-nutrient seedlings. The multi-phasic cycle may involve the interaction of AM and host growth, relative carbon allocation (root: shoot ratios), root colonization, soluble sugars, starch and P, arbuscule and vesicle numbers and spore populations (Douds and Chaney, 1986).

The cost-benefit relationship of the AM association for P acquisition (benefit) and carbon expenditures to the hyphae (cost) is not simple. The proportion of root length colonized by AM increased with decreasing nutrient availability (Boerner, 1986; Eissenstat et al., 1993; Graham et al., 1997). However, foliar N and P concentrations in plants from lower fertility sites were as high as or even higher than those in plants from higher fertility sites. This resulted in increased tissue nutrient enrichment ratios with decreasing fertility levels. Translocation of ^{14}C-photosynthates was studied in carrizo citrange (*Poncirus trifoliata X Citrus sinensis)* with split-root system that was one-half mycorrhizal and the other nonmycorrhizal. At higher nutrient levels, supply of P to leaves was similar in one-half and fully-AM plants (Douds et al., 1988). Yet fully-AM plants allocated twice the radiolabeled photosynthate to the mycorrhiza than did the one-half AM plants. It appears that an optimal level of mycorrhizal colonization occurs, above which the plant undergoes no enhanced P acquisition while still continuing to partition photosynthates to the mycobiont. The influence of AM on carbon allocation in plants is more fully reviewed by several workers (Anderson and Rygiewicz, 1991; Eissenstat et al., 1993; Graham et al., 1997).

Mycorrhizal roots are able to obtain more nutrients from soil than non-mycorrhizal roots because hyphal strands exploit a greater volume of soil than roots alone. The vast majority of mycorrhizal research has focused on host responses to nitrogen and phosphorus in crop plants. Several studies have shown that mycorrhizae can influence plant competition, demographics, succession and community structure of plant in pristine ecosystems. Future research should be directed toward the role of AM fungi in relation to nutrient cycling in natural and disturbed ecosystems with emphasis on plant diversity, ecosystem productivity and stability.

ANTHROPOGENIC STRESSES

Anthropogenic stresses can impact mycorrhiza by at least three mechanisms: (1) direct effects on the mycorrhizal roots; (2) effects on the shoot, which alter carbon allocation to mycorrhiza; and (3) nutritional factors

which alter carbon allocation to mycorrhiza (Anderson and Rygiewicz, 1991). Feedback factors are difficult to predict and multiple mechanisms may be involved. However, altered carbon allocation is likely to play a key role in response to these stresses. Indirect effects, acting through altered patterns of carbon allocation, may be a principle mechanism through which stresses impact mycorrhizal roots. Changes in allocation patterns resulting from a change in sink strength or a reduction in nutrient availability, for example, are indicative of impacts of single or multiple pollutant stresses.

A. Compaction

Soil compaction results from heavy machinery used in forest harvesting and agricultural operations (Soane and van Ouwerkerk, 1994). The increasing size and weight of heavy machinery has caused an increased compaction of both forest and agricultural soils. Soil compaction leads to degradation of structure, lower porosity, decreased water potential, increased soil erosion, decreased root growth, and ultimately reduced plant growth (Bengough and Mullins, 1991; Horn and Lebert, 1994). In a greenhouse study, Nadian et al., (1997) found that increase in soil compaction significantly reduced root length, mycorrhizal formation with *Glomus intraradices*, shoot dry weight, P uptake and shoot growth of *Trifolium subterraneum* L. Soil compaction had no significant effect on the fraction of root containing arbuscules and vesicles. Xiao-Lin et al., (1997) also reported that increased soil compaction significantly reduced root density, mycorrhizal formation with *Glomus mosseae*, shoot dry weight, P uptake, and shoot growth of *Trifolium pratense*. In a field study, Entry et al., (1996a) found that soil compaction significantly reduced root length, shoot dry weight, and above-ground biomass of *Zea mays;* it had no significant effect on the fraction of root containing mycorrhizal hyphae, nutrient uptake or yield.

Preliminary research suggests that in agricultural systems, soil compaction from tractor traffic does not seem to reduce AM development in crops planted in sandy soils because they are not growing directly in the area compacted by the tractor wheels. The impact of compaction on AM formation has been investigated primarily in a greenhouse environment and has not been studied in detail. A series of studies that investigate the effects of soil compaction on AM formation and function on several plant species and range of soil types could be a valuable contribution to the literature.

B. Heavy Metals

The heavy metal content of soils is derived in part from the chemical nature of the parent material of the soils. In some areas, it may be derived from dry and wet atmospheric deposition as dusts and water droplets (Adriano, 1986; Dosskey and Adriano, 1992). Sources of the heavy metals in dusts and droplets include wind and water movement of polluted soils, acid rain and fogs, and volcanic eruptions. Anthropogenic atmospheric sources of heavy metals include mining, smelting, industrial and agricultural activities, burning of fossil fuels, land clearing, and incineration of municipal wastes. Direct addition of municipal sludges is also a source of heavy metals to soils.

Availability and toxicity of heavy metals to plants and mycorrhizal fungi varies, depending on the actual concentrations and oxidation state of metals, pH, cation exchange capacity, texture, organic matter content and redox potential of soil (Adriano, 1986; Dosskey and Adriano, 1992). In roots, heavy metals such as aluminium can impair cell division, increase cell wall rigidity, alter root respiration, precipitate nucleic acids, and interfere with the uptake and transport of Ca, Mg, P, and Fe (Foy, 1983). Fungal hyphae sequester heavy metals, which may serve to reduce movement into and toxicity to the host and thus help in stress tolerance (Morselt et al., 1986; Entry et al., 1987; Jones and Hutchinson, 1988). Detoxification mechanisms may enable plants and AM fungi to avoid the toxic effects of heavy metals.

Addition of inorganic or organic amendments to culture media or soils and resultant competitive or binding interactions may also affect metal toxicity to AM fungi or plants (Timmer and Raddon, 1980; Dosskey and Adriano, 1992; Smith and Read, 1997). Biological factors likely to affect the bioavailability and potential toxicity of heavy metals to AM fungi and plants include plant and fungal genus, species, genotype, ecotype as well as interactions between plants and mycorrhizal fungi and other rhizosphere or soil microbes (Gildon and Tinker, 1983; Baker and Walker, 1989; Kothari et al., 1991; Diaz et al., 1996).

Due, in part, to the continuing limitations in axenic culture of AM fungi, there are few reports on the direct effects of heavy metals on AM fungi. Gildon and Tinker (1983) reported on differences in the sensitivity of *Glomus* sp. to heavy metals; the germination and growth of isolates obtained from heavy metal contaminated soils tended to be more tolerant to higher concentrations of metals in agar media. In greenhouse and field studies, Leyval et al., (1995) found generally lower spore numbers, mycorrhizal infectivity potential and germination of spores isolated from more contaminated soils. There was also a delay in colonization in soils with increased heavy metal content.

As reviewed in Gadd (1993) and Leyval et al., (1997), most reports have described a positive effect of mycorrhizal inoculation on growth of plants in heavy-metal contaminated soils, particularly ectomycorrhizal hosts such as species of *Pinus*. This protective benefit may be related to the adsorptive or binding capability for heavy metals of the relatively large fungal biomass associated with host plant roots, which may physically minimize or exclude the entry of heavy metals into host plants. Among ericaceous host plants, only those colonized by ericoid mycorrhizal fungi appear to be able to tolerate high levels of heavy metals. Responses to protective effects of AM fungi to heavy metal toxicity among AM host plant species have been varied, but generally positive, depending on host plant and fungal isolate source (Gadd, 1993; Leyval et al., 1997). The actual and available levels of metals in given soils and the degree of host plant mycorrhizal dependence have also been reported to affect the level of plant uptake and tolerance to heavy metals (Diaz et al., 1996).

Mycorrhizal inoculation of plants often results in a reduction of heavy metal toxicity to plants. Diverse biological and physical mechanisms have been proposed to explain the generally lower metal toxicity to plants colonized by AM fungi. These range from adsorption of metals onto plant or fungal cell walls and in plant tissues or onto/into extraradical mycelium in soil (Dueck et al., 1986; Galli et al., 1994), to chelation by fungal or other associated rhizosphere microbial molecules such as siderophores and metallothioniens, or sequestration by plant compounds such as phytochelatins or phytates (Van Steveninck et al., 1987; Joner and Leyval, 1997). Additional heavy metal tolerance mechanisms may include dilution by increased root or shoot growth, exclusion by precipitation onto polyphosphate granules, and compartmentalization into plastics and other membrane-rich organelles (Van Duin et al., 1991; Turnau et al., 1993; Galli et al., 1994).

Both fungal isolates and plants may vary in their individual or combined tolerance to heavy metals. Optimizing the use of AM fungi to permit growth of plants in soils contaminated with heavy metals may require careful selection of specific AM fungal and host plant combinations for given soil conditions. It will also likely require a skilful use of inorganic and organic amendments to maximize plant growth and to capitalize on interactions or competitions between metals and elements such as phosphorus and sulfur, whose uptake is generally enhanced in mycorrhizal plants. For example, increased phosphorus may increase plant biomass and thus perhaps detoxify the potential effects of heavy metals by dilution or precipitation or adsorption of heavy metals onto polyphosphate granules could serve as a detoxification or tolerance mechanism for plants. The non-target ecological effects of plants or fungi which result in adsorption, translocation and sequestration of heavy metals also

need to be considered in parallel with efforts to revegetate soils contaminated with high levels of heavy metals. Efforts to phytoremediate, reclaim or restore vegetation to soils contaminated with heavy metals, by use of mycorrhizal plant species and inocula is gaining acceptance. In this context, evaluation of the potential effects on invertebrate and vertebrate aboveground and belowground consumers of plant and fungal tissues and structures on soil food web biota and on plant community composition in surrounding areas also need to be considered (Entry et al., 1996b).

Given the elusive status of aseptically propagating axenic cultures of AM fungi, research on methods to grow and genetically characterize, develop and select AM fungi in pure laboratory cultures continue to be a priority. The lack of correlation between AM fungal colonization rates and beneficial or detrimental host response perhaps suggests a need to look more closely at the diversity and competition among AM fungi colonizing given roots or plants. Identification and culture of the most effective isolates could then be used to select or develop genetically improved strains customized for given soil conditions or host plants.

C. Organic Pollutants

1. Pesticides

Research involving the interaction of toxic organic pollutants, including pesticides, with AM has been largely limited to assessing effects of fungicides on mycorrhizal formation and phosphorus uptake. Interaction of multiple fungicides on the function of mycorrhiza is important in the context of minimizing the effect of plant pathogens while maximizing the influence of mycorrhizal contribution to plant nutrition (Sukarno et al., 1996). Several workers have found that benomyl inhibited AM infection and phosphorus uptake in crop plants. Sukarno et al., (1996) reported that 31.25 mg benomyl kg^{-1} soil (manufacturers recommended rates) reduced the formation of *Glomus* sp. with onion (*Allium cepa* L.) and phosphorus assimilation by the plant. Larsen et al., (1996) also reported that 10 mg benomyl kg^{-1} soil reduced formation of *Glomus caledonium* with *Cucumis sativus* roots. Merryweather and Fitter (1996) found that 63 mg benomyl kg^{-1} inhibited AM colonization on *Hyacinthoides non-scripta* (bluebell). AM formation resulted in a lower P uptake by the plant. Reduced mycorrhizal formation in annual grasses with benomyl resulting in reduced plant biomass has also been reported; phosphorus assimilation by the plants was, however, not affected (Carey et al., 1992; West et al., 1993; Newsham et al., 1994).

Fumigation of soil with methyl bromide inhibits AM formation and phosphorus uptake in all plants that have been studied. Jawson et al.,

(1993) reported that soil fumigation with methyl bromide substantially reduced mycorrhizal formation in corn roots to a depth of 15 cm; below 15 cm however roots became mycorrhizal. Afek et al., (1991) found that fumigation of soil with methyl bromide inhibited AM formation in cotton, onion and pepper (*Capsicum annuum* L.), however, if soil was inoculated with spores of *G. intraradices* after fumigation, these plant species had higher percentages of roots colonized by mycorrhizae and greater plant biomass. Buttery et al., (1988) found that methyl bromide fumigation of soil reduced AM formation and phosphorus uptake in pea (*Phaseolus vulgaris* L.) and soybean (*Glycine max* L.). Hass et al., (1987) also reported that methyl bromide fumigation inhibited AM formation in pepper. Brown et al., (1974) and Menge (1982) reported that methyl bromide fumigation inhibited mycorrhizal formation and phosphorus uptake in wheat (*Triticus aesivium* L.) and potato (*Solanum tuberosum* L.). Several workers have reported that application of fosetyl-Al (aliette) reduced root growth, but stimulated mycorrhizal formation and phosphorus uptake by crop plants (Clark, 1978; Jabaji-Hare and Kendrick, 1985; 1987; Despite et al., 1989; Sukarno et al., 1993, 1996). However, application of 12.5 mg ridomil kg^{-1} soil did not reduce *Glomus* sp. formation with onion roots.

2. Polychlorinated Aliphatic and Phenolic Compounds

There are several recent studies concerning phytoremediation of chlorinated phenolic compounds such as chloroacetamide herbicides in soil (Hoagland et al., 1997), the deicing agent ethylene glycol (Rice et al., 1997), trichloroethylene with hybrid poplars (Gordon et al., 1997), polyaromatic hydrocarbons (Qiu et al., 1997) and chlorinated phenols (Ensley et al., 1997). However, few published studies have examined the influence of organic pollutants on the efficacy of AM fungi to degrade these chemicals (Donnelly et al., 1993; Donnelly and Fletcher, 1995; Gaskin and Fletcher, 1997; Watrud and Seidler 1998).

Large areas of land have been contaminated by various types of organic pollutants and heavy metals. Remediation of soil contaminated with pollutants requires that soil be removed from the site and treated with various dispersing and chelating chemicals. Transport of soil requires heavy equipment, is time consuming and expensive. Furthermore, it may also result in additional dispersal of pollutants through possible spills or leaks (Entry et al., 1996a). The cost to clean up many of these sites is often prohibitive and, therefore, limited attempts have been made to remediate many of these sites. In contrast, phytoremediation may not only remediate a site, but may eventually reclaim it, by fostering the establishment of a plant community. Phytoremediation of soil contaminated with pollutants is an emerging science and one where mycorrhizal relationships are of crucial importance.

CONCLUSIONS

Arbuscular mycorrhizal fungi are of interest for their reported role in alleviation of diverse soil associated plant stress factors. The majority of plant stress-mycorrhizal research has investigated the impact of extremes in water, temperature, pH and inorganic nutrient availability on mycorrhizal formation and nutrient aquisition. There has been increased emphasis in agricultural and forest research on sustainable systems with emphasis on soil quality. However, there is scarcity of research on the role that AM play in stability and resilience of these ecosystems.

Arbuscular mycorrhizae have the ability to alleviate many anthropogenic derived plant stresses, including heavy metals and the degradation of polychlorinated aliphatic and phenolic pollutants. The efficacy of plant-mycorrhizal associations to remediate soils contaminated with toxic pollutants is an area that can directly benefit the society and deserves increased emphasis. Before the full potential benefits of AM fungi to host plants and in reclamation of soils with adverse physical and chemical conditions can be realized, research advances are needed in the axenic culture, genetic development, and physiology of these ubiquitous symbionts.

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