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Influence of adverse soil conditions on the formation and function of *Arbuscular mycorrhizas*☆

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Abstract

The majority of plants have mycorrhizal fungi associated with them. Mycorrhizal fungi are ecologically significant because they form relationships in and on the roots of a host plant in a symbiotic association. The host plant provides the fungus with soluble carbon sources, and the fungus provides the host plant with an increased capacity to absorb water and nutrients from the soil. Adverse conditions are a pervasive feature in both natural and agronomic soils. The soil environment is constantly changing with regard to moisture, temperature and nutrient availability. In addition, soil properties are often manipulated to improve crop yields. In many cases, soils may be contaminated through disposal of chemicals that are toxic to plants and microorganisms. The formation and function of mycorrhizal relationships are affected by edaphic conditions such as soil composition, moisture, temperature, pH, cation exchange capacity, and also by anthropogenic stressors including soil compaction, metals and pesticides. Arbuscular mycorrhizal fungi are of interest for their reported roles in alleviation of diverse soil-associated plant stressors, including those induced by metals and polychlorinated aliphatic and phenolic pollutants. Much mycorrhizal research has investigated the impact of extremes in water, temperature, pH and inorganic nutrient availability on mycorrhizal formation and nutrient acquisition. Evaluation of the efficacy of plant–mycorrhizal associations to remediate soils contaminated with toxic materials deserves increased attention. Before the full potential benefits of arbuscular mycorrhizal fungi to reclaim contaminated soils can be realized, research advances are needed to improve our understanding of the physiology of mycorrhizae subjected to adverse physical and chemical conditions. This paper will review literature and discuss the implications of soil contamination on formation and function of arbuscular mycorrhizal associations. © 2002 Elsevier Science Ltd. All rights reserved.

Keywords: Arbuscular mycorrhizas; Fungi; Soil; Stress

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1. Introduction

Mycorrhizal fungi are ecologically significant because they form relationships in and on the roots of a host plant in a symbiotic association. The host plant provides the fungus with soluble carbon sources, and the fungus provides the host plant with an increased capacity to absorb water and nutrients from the soil. It has been found that the majority of plants do have mycorrhizal fungi associated with them; some of these associations are very specific while others are very broad. Ninety to 95% of all land plants form some type of mycorrhizal association so that mycorrhizas, not roots are the chief organs of nutrient uptake by plants (Bago et al., 2000; Smith and Read, 1997). Mycorrhizal fungi are classified into one of the following four major types: ectomycorrhizas, arbuscular mycorrhizas, ericaceous mycorrhizas, and orchid mycorrhizas. Classification of mycorrhizal associations are more fully described in several recent publications (Sylvia et al., 1998; Smith and Read, 1997). Arbuscular mycorrhizal fungi are characterized by the presence of fungal hyphae within the root cells, the absence of a Hartig net, and the presence of fungal hyphae on the root surface but not as a fungal sheath. Arbuscules, branched hyphae found inside the root cells, constitute the area of nutrient exchange between the fungus and the host plant. Arbuscular mycorrhizal associations are the most abundant of the several different types of mycorrhizas. They are formed by a wide variety of host plants, including angiosperms, gymnosperms, pteridophytes and some mosses, lycopods and psilotales with a relatively small group of aseptate filamentous fungi (Bago et al., 2000).

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 vigor and extent of mycorrhizal formation. This lack of understanding arises in large part from the difficulty of studying the intact association, which is a functionally and anatomically distinct structure comprised of two biologically different organisms (e.g. plants and arbuscular mycorrhizal fungi). Adverse conditions are a pervasive feature in both natural and agronomic soils. The soil environment is constantly changing with regard to moisture, temperature and nutrition. In addition, soil properties are often manipulated to improve crop yields and, in many cases, soils may be contaminated through disposal of chemicals that are toxic to plants and microorganisms. The formation and function of mycorrhizas are affected by edaphic conditions such as soil composition, moisture, temperature, pH, cation exchange capacity and anthropogenic abiotic and biotic stresses including soil compaction, metals and pesticides.

Levitt (1980) defined stress avoidance as mechanisms by which an organism may reduce the impact of the stress, while stress tolerance permits an organism to simply endure the adverse environment. Levitt's definition of stress can be modified to include any environmental factor with the capacity to elicit a chemical or physical change (metabolic adjustment), regardless of whether the change is beneficial or detrimental to the organism. An organism's response to stress may involve interactions among various avoidance and tolerance mechanisms (Tingey and Anderson, 1991; Tingey and Taylor, 1982; Taylor, 1978). 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 with the stress' without being killed (Levitt, 1980). The site of action of a pollutant stress varies and can be the mycorrhizas, roots or shoots. The site of action will determine whether the primary response occurs in the fungus or the shoot.

Several publications that have reviewed the impact of various stresses on plant–mycorrhizal interactions (Augé, 2001; Meharg and Cairney, 2000; Cairney and Meharg, 2000; Sylvia and Williams, 1992; Andersen and Rygiewicz, 1991; Read, 1991; Van Duin et al., 1991) will provide additional information on this subject.

2. Natural stressors

Soils rarely provide ideal conditions for growth and survival of plants and soil microorganisms. Since soil conditions are constantly changing, the soil environment may favor development of arbuscular mycorrhizas at one point in time, and inhibit them at another time. The influence of moisture and temperature are examples of these effects. Adequate soil moisture and temperature may favor development of arbuscular mycorrhizas. However, when soil moisture or temperature become too high or low, mycorrhizal formation may be inhibited. 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.

Many studies show that natural and anthropogenic factors may have an impact on carbon allocation in both mycorrhizal and non-mycorrhizal plants by a variety of mechanisms.

2.1. Moisture stress

Either high or low levels of water can be stresses to plants. Plant response to colonization by arbuscular mycorrhizal fungi depends on the severity and periodicity of drought and other edaphic conditions. Arbuscular mycorrhizal fungi may affect host plant function and productivity under both high and low moisture conditions (Augé, 2000). In growth chamber studies, Subramanian and Charest (1997, 1999), Ming and Hui (1999), and Bryla and Duniway (1997a,b) found that plant moisture deficits of −1.5 to −2.0 MPa did not affect mycorrhizal colonization or phosphorus uptake by *Triticum aestivum*, *Hippophae rhamnodies* or *Zea mays*. In greenhouse studies, both Subramanian and Charest (1995, 1999) and Schellenbaum et al. (1998) found that drought-stressed maize infected with *Glomus mosseae* (Nicol. and Gerd.) or *G. intraradices* (Schenck and Smith, 1982) had higher concentrations of glucose, fructose and total amino acids in leaves and roots than non-mycorrhizal plants. After applying periods of drought stress of varying length and severity, Ellis et al. (1985) found that arbuscular mycorrhizal colonization increased leaf area, total plant and root biomass, number of tillers, and grain yield of wheat. The arbuscular mycorrhizal symbiosis also increased biomass of two native forb species [*Baptisia australis* (L.) R. Br. and *Liatris aspera* Michx.] experiencing moisture deficit regardless of levels of fertilizer added, compared with non-mycorrhizal plants (Zajicek et al., 1987). Simpson and Daft (1990) found moisture deficits increased colonization percentages of roots and reduced spore production when the arbuscular mycorrhizal fungi *Acaulospora* and *Glomus* spp formed associations with corn (*Zea mays* L. cv Drocan PO1) or sorghum (*Sorghum bicolor* L. cv CSH5). Sylvia et al. (1993a) conducted field studies to examine the effects of arbuscular mycorrhizal drought-stressed *Z. mays*. Grain yield and total above-ground biomass responded positively to irrigation for both mycorrhizal and non-mycorrhizal plants. However, when plant moisture deficit increased, grain yield and above-ground biomass was significantly higher in mycorrhizal plants.

The arbuscular mycorrhizal symbiosis may alleviate plant responses to moderate moisture deficit by several mechanisms including increased water uptake from the soil by hyphae (Al-Karaki and Al-Raddad, 1997; Davies et al., 1992; Augé et al., 1992), altered hormonal levels causing changes in stomatal conductance (Drüge and Schönbeck, 1992), increased turgor by lowering leaf osmotic potential (Augé et al., 1986; Davies et al., 1993), improved nutrition of the host (Johnson and Hummel, 1985; Fitter, 1988), and improved plant recovery after drought by maintaining the soil–root continuum (Reid, 1979; Sweatt and Davies, 1984). Some research has shown that drought response of mycorrhizal plants can be independent of plant nutrition, i.e. phosphorus (Bethlenfalvay et al., 1988; Peña et al., 1988; Sánchez-Díaz et al., 1990; Henderson and Davies, 1990; Davies et al., 1993). Recently, Goicoechea et al. (1995) suggested that arbuscular mycorrhizae were important in maintaining cytokinin levels under drought. When alfalfa (*Medicago sativa*) 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 the different drought responses of the two types of plants were mediated by leaf cytokinin concentrations.

2.2. Flooding

Compared with the amount of work done on moderate moisture deficit, less research has been done on effects of excess water (Keely, 1980; Hartmond et al., 1987). The arbuscular mycorrhizal symbiosis has been found on aquatic and wetland plants (Dhillion and Ampornpan, 1992; Tanner and Clayton, 1985; Ho, 1987; Clayton and Bagyaraj, 1984; Chaubal et al., 1982; Bagyaraj et al., 1979; Sondergaard and Leagaard, 1977; Read et al., 1976). Arbuscular mycorrhizas have not been found in aquatic macrophytes in the families Cyperaceae and Juncaceae (Allen, 1991; Anderson et al., 1984; Harley and Smith, 1983; Kahn, 1974), except as mycelial colonization in the rhizosphere and infrequently as deposits in root epidermal cells (Powell, 1975). Anderson et al. (1984) did not find arbuscules in putative mycorrhizas in plants growing in the wettest habitats along a soil moisture gradient, however, some of the plants growing in moist sites were mycorrhizal. Many wetland species had increased arbuscular mycorrhizal fungal colonization during the drier seasons (Rickerl et al., 1994). Higher rates of arbuscular mycorrhizal colonization were found in moist soil compared with rates found in very dry or flooded soils (Miller, 2000; Miller and Sharitz, 2000; Miller and Bever, 1999; Lodge, 1989). Several investigators found that the number of arbuscular mycorrhizal spores in soil were not affected by extended flooding indicating that mycorrhizal formation is related to plant growth (Miller, 2000; Miller and Sharitz, 2000; Ellis, 1998). Wetzel and van der Valk (1996) measured arbuscular mycorrhizal colonization for 19 plant species growing in several vegetation zones in six wetlands. Each of the six wetlands could be assigned to 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 (low prairie, wet meadow, shallow emergent). They did multiple regression analyses to evaluate the significance of environmental factors and arbuscular mycorrhizal colonization. Their analyses indicated that host plant species, soil phosphorus, and soil pH influenced fungal colonization. Many of these observations may be explained by soil redox potential. The numbers of mycorrhizal spores in wetland soils have been positively correlated to redox potentials (Kahn, 1993b). Spores were abundant in upland terrestrial soils, moderately abundant to rare in wetland soils and rare to absent in water (Kahn, 1993a; Stevens and Peterson, 1996). Spore germination was inhibited at low O_2 concentrations, and germination returned to previous percentages when O_2 concentrations were returned to normal (LeTacon 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 the reducing environments of flooded soils (E_{h} œ 150 mV) than in more aerobic soils (E_{h} Æ 300 mV).

Mycorrhizal *Casurina equisetifolia* (J.R. and G. First) seedlings adapted to flooding better than non-inoculated seedlings because of the greater number of adventitious roots and hypertrophied lenticles which increased O_2 availability in the root zone (Osundina, 1998). 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 (Jaynes and Carpenter, 1986). The Fe-OH sheath around roots is a common characteristic of plants growing in anoxic soils (St.-Cyr et al., 1993). When flooding was intermittent and the soil was wet with a high redox (E_{h} Æ 300 mV), plants were mycorrhizal. However, when flooding was continuous, and redox low (E_{h} œ 150 mV) mycorrhizal associations were less likely to form.

A more thorough review concerning mycorrhizal formation and function in wetland ecosystems is found in Kahn and Belik (1995). Even though arbuscular mycorrhizal fungi are thought to be critical in nutrient accumulation and, therefore, in the functioning of wetland and aquatic ecosystems (Miller, 2000; Miller and Sharitz, 2000; Miller and Bever, 1999; Wigland and Stevenson, 1994, 1997; Tanner and Clayton, 1985), this area of research has received little attention.

2.3. Temperature

In general, arbuscular mycorrhizae form in temperatures ranging between 18 and 40°C with the optimum for most fungal–host species near 30°C. The optimal range for the intact symbiosis depends on the temperatures controlling fungal germination, photosynthesis and carbon flow to roots. However, the influence of temperature on arbuscular mycorrhizal plants is variable and appears related to the exact fungal–host species combination as well as the developmental stage of the plant. Spores of AM fungi differ in their optimum germination temperatures (Saif, 1983; Schenck et al., 1975; Schenck and Schroder, 1974; Matsubara and Harada, 1996). Soil temperature along with soil moisture will exert a major influence on mycorrhizal colonization of plants (Braunberger et al., 1997). At constant temperatures, mycorrhizal colonization of asparagus (*Asparagus officinalis* L.) was highest at 25°C. When inoculated with *G. etunicatum* and at 25–30°C when inoculated with *Gigaspora margarita* (Matsubara and Harada, 1996). Maximum arbuscular development in soybean [*Glycine max* (L.) Merr.] roots occurred at 30°C with *Endogone gigantea* Nicol. and Gerd., maximum mycelial development in roots occurred at 28–34°C, and maximum sporulation and vesicle development occurred at 35°C (Schenck and Schroder, 1974). The efficacy of mycorrhizas 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. Arbuscular mycorrhizal formation was related to the various combinations of soil temperatures and fungal species. Infected root length and number of vesicles increased as temperature increased from 20 to 30°C in *Eupatorium odoratum* L. inoculated with *G. macrocarpus*, while arbuscular development decreased above 25°C (Saif, 1983). Furlan and Fortin (1973) found that arbuscular mycorrhizal 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; Smith and Roncadori, 1986). However, maximum growth was at 36°C when plants were inoculated with *G. ambisporum* (Schenck and Smith, 1982). In ash (*Fraxinus pennsylvanica* Marsh.), Andersen et al. (1987) found greater relative leaf area and growth rates of arbuscular mycorrhizal 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 non-mycorrhizal 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* [(Buchanan) Jordan] 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, colonization was inhibited. The optimal temperature for the arbuscular mycorrhizal fungus was not necessarily optimal for nodulation and N_2 fixation, which ranged from 25 to 30°C in this study (Zhang et al., 1995). The arbuscular mycorrhizal fungus negatively affected nodule numbers at lower temperatures, while it positively affected numbers at higher temperatures. The smaller number of nodules at the lower temperatures was offset by increased specific nodule mass such that the endophyte stimulated N_2 fixation at the lower root zone temperatures. They 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 fungus and the N_2-fixing bacterium occurring at lower root zone temperatures.

2.4. pH

Arbuscular mycorrhizal fungi responded to pH in a highly variable fashion. The response of arbuscular mycorrhizal plants to pH has been studied for some very practical reasons including potential negative effects of H^+ on plant productivity via direct effects on the endophyte and host plant physiology, and indirect effects via changes in soil processes, e.g. metal and base cation availability (Clark et al., 1999a,b; Habte and Soedarjo, 1996). Some AM fungi did poorly in low-pH soils, while other fungi did poorly after acid-soils were limed (Mosse, 1972a,b). Yet, in other studies, plants forming associations with arbuscular mycorrhizal fungi had improved plant growth in acid soils that were limed (Clark et al., 1999a,b; Davis et al., 1983), while in other acid soils, a positive AM fungal effect was found without the need to increase pH (Guzman-Plazola et al., 1988).

Arbuscular mycorrhizal fungi play an important role in improving plant productivity by enhancing the nutrient uptake, particularly phosphorus (P) (Clark et al., 1999a,b; Smith and Read, 1997; Bago et al., 1996). The influence of the symbiosis in nutrient absorption depends on the uptake capabilities of the host and the endophyte, extent of colonization of the root and the surrounding soil, and factors affecting the formation and reproduction of the endophyte symbiosis (Habte, 1995; Wang et al., 1985). The H^+ activity affects 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 of cation absorption (e.g. NH_4^+ — Clark et al., 1999a; Frey and Schüepp, 1993; Johansen et al., 1992, 1993a,b) and anions (e.g. NO_3^- — Clark et al., 1999b; Bago et al., 1996; Tobar et al., 1994) by arbuscular mycorrhizal fungi appear similar to those found in other organisms. Some researchers have suggested that mycorrhizal fungi tolerate adverse external pH conditions by modifying the pH of the mycorhizosphere during the uptake process (Pacovsky, 1986; Tinker, 1975). It may be that the effect of soil pH on arbuscular mycorrhizal fungi and inoculated plants may depend on the difference between the pH of the soil from which a fungus is obtained and the pH of the experimental system under study. In short, some mycorrhizal fungi may not readily adapt to soils with a pH unlike that of the soil of their origin, thus pH may constrain establishment of arbuscular mycorrhizas. Studies suggesting that this relationship may exist involved the direct liming of soils (Kucey and Diab, 1984; Newbould and Rangeley, 1984), analyses of arbuscular mycorrhizas across diverse soil types (Sylvia et al., 1993b; Menge et al., 1982; Skipper and Smith, 1979), and various management treatments that included fertilizing or physically modifying the soil (e.g. organic amendments, Soedarjo and Habte, 1993).

Sylvia and Williams (1992) indicate that it is not clear if arbuscular mycorrhizal fungi offer any protection to host plants against detrimental effects of adverse pH conditions. Klironomos (1995) speculated that AM 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 favorable for arbuscular mycorrhizal fungi, and generally support ectomycorrhizal associations. Brunisols and luvisols are considered more favorable for arbuscular mycorrhizal fungi. In luvisolic soils, various 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 arbuscular mycorrhizal fungi characteristics found in some podzolic soils by Klironomos (1995) may be indicative of stress (Duckmanton and Widden, 1994; Spitko et al., 1978). These results indicate that many arbuscular mycorrhizal fungi have the capability to tolerate low pH conditions. The response of arbuscular mycorrhizas to soil pH seems to be dependent primarily on the fungal species. Some fungal species readily form arbuscular mycorrhizas in low-pH soils, while other species form mycorrhizas in higher pH soils. The question posed by Sylvia and Williams (1992) concerning the adaptability of arbuscular mycorrhizal fungi to soil conditions different from 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.

2.5. Nutrients

Arbuscular mycorrhizas enhance plant acquisition of nutrients by increasing the absorptive surface area of the uptake system. Mycorrhizal roots are able to obtain more nutrients from nutrient-deficient soils than are non-mycorrhizal roots because hyphae exploit a greater volume of soil than roots alone. Mycorrhizas are especially important for plant survival and growth when the soil has low concentrations of plant available nutrients, especially P (George, 2000; Joner et al., 2000a; Liu et al., 1998; Harrison and van Buuren, 1995; Eckhard et al., 1992; Faber et al., 1991; Graham et al., 1991). Quantification of mycorrhizal contributions to plant uptake of nutrients is difficult, because of the varying responses of different plant growth developmental stages to changing environmental conditions (George, 2000). In a simplified example, 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 absorption rate exceeds its diffusion rate or the rate at which it moves toward the absorbing surface, 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 (Harley, 1989). A deficiency zone will develop around the absorbing surface. At this point, the rate of uptake diminishes because it is dependent on the rate at which it moves (diffuses) through the soil.

Most research on arbuscular mycorrhizas has focused on cultivated crop plant responses, rather than on plants in natural ecosystems. Work in natural ecosystems has shown that arbuscular mycorrhizas will influence plant competition and succession, thus affecting the functioning and stability of an ecosystem (Smith et al., 1999; Van der Heijden et al., 1998a,b; Wilson and Hartnett, 1998, 1997; Francis and Read, 1994; Hartentt et al., 1994; Gange et al., 1993; Goldberg and Barton, 1992; Allen, 1991; Read, 1991; Fitter, 1989). In tall grass prairies, warm season grasses are more dependent than cool season grasses on the mycorrhizal symbiosis (Wilson and Hartnett, 1997; Hetrick et al., 1988, 1990). 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, 1998, 1997). Since there is normally a great deal of plant diversity in natural ecosystems, the presence or absence of arbuscular mycorrhizal fungi in soils can change the competitive balance between obligately-mycorrhizal, facultatively-dependent and non-dependent plant species, and consequently, the species composition and productivity of the ecosystem.

The response of arbuscular mycorrhizal plants grown under varying nutrient regimes has been characterized by a multi-phasic phenology where changes in gross plant morphology between inoculation treatments do not become apparent until the second growing season (Douds and Chaney, 1986). At that time, differences in plant development caused by different nutrient treatments were related to mycorrhizal colonization levels, which increased for low-nutrient seedlings and decreased in high-nutrient seedlings. The multi-phasic cycle response may involve the interaction of the fungus and host growth with regard to carbon allocation, root colonization, content of soluble sugars, starch and P in the root, arbuscule and vesicle numbers, and spore populations (Douds and Chaney, 1986).

Interpreting the cost–benefit relationship of the arbuscular mycorrhizal symbiosis for P acquisition (benefit) and carbon expenditures to the hyphae (cost) is not simple. The proportion of root length colonized by the fungus increases with decreasing nutrient availability (Graham et al., 1997; Eissenstat et al., 1993; Boerner, 1986). However, foliar N and P concentrations in plants from lower fertility sites can be as high as, or higher than, those in plants from higher fertility sites. Translocation of ^{14}C-photosynthates was studied in carrizo citrange (*Poncirus trifoliata* L. Raf *X Citrus sinensis L.*) in split-root systems where both sides were mycorrhizal, one-half was mycorrhizal and the other non-mycorrhizal, or both sides were non-mycorrhizal. At higher nutrient levels, supply of P to leaves was similar in one-half-inoculated and the fully-mycorrhizal plants (Douds et al., 1988). Yet fully-mycorrhizal plants allocated twice the radiolabeled photosynthate to mycorrhizas than did the one-half-mycorrhizal plants. Apparently, an optimal level of colonization can occur, above which the plant does not receive P but still continues to allocate photosynthate to the fungus. The influence of mycorrhizas on carbon allocation in plants is more fully reviewed by Graham et al. (1997), Eissenstat et al. (1993) and Andersen and Rygiewicz (1991).

The vast majority of arbuscular mycorrhizal research has focused on responses to N and P in crop plants. Some studies have shown that mycorrhizas can influence plant competition, demographics, succession, and community structure in native ecosystems. Future research should be directed toward understanding the influence of arbuscular mycorrhizas to modify nutrient cycling and acquisition in natural and disturbed ecosystems with regard to plant diversity, and ecosystem productivity and stability.

3. Anthropogenic stressors

Anthropogenic stresses such as soil compaction, and metal and organic contamination can affect arbuscular mycorrhizas by at least three mechanisms: (1) direct effects on mycorrhizal roots; (2) through effects on the shoot, which alter carbon allocation to mycorrhizas; and (3) nutritional factors which alter carbon allocation to mycorrhizas (Andersen and Rygiewicz, 1991). Feedbacks, and direct and indirect interactions between plant hosts and arbuscular mycorrhizal fungi are difficult to predict, especially since multiple mechanisms may be involved. However, altered carbon allocation is likely to play a key role in the response to many, if not most, of these stresses. Indirect effects, acting through altered patterns of carbon allocation, may be a principal 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 pollutant stresses. We will review the effects of a number of anthropogenic soil-associated stresses including, metals, agricultural practices and pesticides on arbuscular mycorrhizal development and function and on host plant tolerance to these stresses.

3.1. Compaction

Soil compaction results from machinery used in forest harvesting and agricultural operations (Soane and van Ouwerkerk, 1994). The use of increasingly larger machinery is causing increases in compaction of both forest and agricultural soils. Soil compaction leads to a 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, Yano et al. (1998) found that increasing soil compaction reduced root length, mycorrhizal formation with *Gigaspora margarita,* root dry weight, P uptake and shoot growth on *Cajanus cajan* L. Nadian et al. (1997) obtained similar results: increasing soil compaction significantly reduced root length, mycorrhizal formation with *G. intraradices,* root dry weight, P uptake and shoot growth of *Trifolium subterraneum* L. Soil compaction had no significant effect on the proportion of roots containing arbuscules and vesicles. Li et al. (1997a,b) also found increasing soil compaction significantly reduced root density, mycorrhizal formation with *G. mosseae,* shoot dry weight, P uptake, and shoot growth of *Trifolium pratense* L. 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* L. However, soil compaction had no significant effect on the proportion of root containing mycorrhizal hyphae, nutrient uptake or yield.

In agricultural systems, soil compaction from tractor traffic did not seem to reduce arbuscular mycorrhizal development on crops grown in sandy soils because tractor wheels do not significantly alter soil bulk density (Entry et al., 1996a). The effects of compaction on arbuscular mycorrhizal formation have been investigated primarily in greenhouse environments and have not been studied in detail in the field. A series of studies that investigates the effects of soil compaction on arbuscular mycorrhizal formation and function on several plant species and across a range of soil types would be a valuable contribution to the literature.

3.2. Metals

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

Availability and toxicity of metals to plants and mycorrhizal fungi varies, depending on the actual concentrations and oxidation states of the metals; soil and rhizosphere pH; and soil cation exchange capacity (CEC), texture, organic matter content, and redox potential (Meharg and Cairney, 2000; Liu et al., 2000; Cairney and Meharg, 2000; Dosskey and Adriano, 1992; Adriano, 1986). In roots, metals such as aluminum 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 metals, which may serve to reduce movement into, and toxicity to, the host (stress tolerance) (Joner et al., 2000b; Meharg and Cairney, 2000; Leyval et al., 1997; Weissenhorn and Leyval, 1996; Weissenhorn et al. (1994)). Detoxification mechanisms enable the plant and fungus to avoid toxic effects.

Addition of inorganic or organic amendments to culture media or soils and resultant competitive or binding interactions for adsorption sites also may alter the effective level of metal toxicity (Joner et al., 2000b; Smith and Read, 1997; Shetty et al., 1994, 1995; Dosskey and Adriano, 1992; Gildon and Tinker, 1983a,b; Timmer and Leyden, 1980). Biological factors proposed to affect bioavailability and potential toxicity of metals to arbuscular mycorrhizal fungi and plants include plant and fungal genera, species, genotype and ecotype as well as interactions between plants and mycorrhizal fungi and other rhizosphere or bulk soil microbes (Díaz et al., 1996; Shetty et al., 1994; Kothari et al., 1991; Baker and Walker, 1989; Gildon and Tinker, 1983b)

Due partly to the long-standing limitations of using axenic cultures to study arbuscular mycorrhizal fungi, there are few reports on direct effects of metals. Gildon and Tinker (1983c) reported on differences in sensitivity of *Glomus* sp. to metals. They found that germination and growth of isolates obtained from metal-contaminated soils tended to be more tolerant to higher concentrations of metals in agar media than isolates obtained from sites with low metal concentrations. In greenhouse and field studies, Leyval et al. (1995) generally found lower spore numbers, mycorrhizal infectivity potential and germination of spores isolated from more contaminated soils compared with fungi obtained from less contaminated sites. They also reported a delay in colonization in soils with increased metal content.

Most reports note a positive effect of mycorrhizal inoculation on growth of plants in metal-contaminated soils. This protective benefit may be related to the adsorptive or binding capability for metals of the relatively large fungal biomass associated with host plant roots, which may physically minimize or exclude the entry of metals into host plants (Joner et al., 2000b; Meharg and Cairney, 2000; Cairney and Meharg, 2000; Hildebrandt et al., 1999; Leyval et al., 1997; Gadd, 1993). Protective responses of arbuscular mycorrhizal fungi to metal toxicity among arbuscular mycorrhizal plants have been variable, but generally existent, depending on host plant and fungal isolate sources (Joner et al., 2000b; Meharg and Cairney, 2000; Hildebrandt et al., 1999; Kaldorf et al., 1999; Leyval et al., 1997; Gadd, 1993). Sharples et al. (2000) reported that *Calluna vulgaris* L. inoculated with *Hymenoscyphus ericae* took up phosphate while excluding arsenate. Killham and Firestone (1983) reported a deleterious effect of arbuscular mycorrhizal inoculation on sensitivity of host plants to metals. The actual and available levels of metals in a given soil, and the degree of host plant mycorrhizal dependence have also been reported to affect extent of plant uptake of, and tolerance to, metals (Martino et al., 2000; Sharples et al., 2000; Kaldorf et al., 1999; Heggo and Angle, 1990; Shetty et al., 1994; Díaz et al., 1996).

Several biological and physical mechanisms have been proposed to explain the generally lower metal toxicity to plants colonized by arbuscular mycorrhizal fungi. These include adsorption onto plant or fungal cell walls present on and in plant tissues or onto or into extraradical mycelium in soil (Joner et al., 2000b; Meharg and Cairney, 2000; Hildebrandt et al., 1999; Kaldorf et al., 1999; Gildon and Tinker, 1983a; Dueck et al., 1986; Dehn and Schüepp, 1989; Galli et al., 1994), chelation by such compounds as siderophores and metallothionens released by fungi or other rhizosphere microbes, and sequestration by plant-derived compounds like phytochelatins or phytates (Joner and Leyval, 1997; Van Steveninck et al., 1987). Other possible metal tolerance mechanisms include dilution by increased root or shoot growth, exclusion by precipitation onto polyphosphate granules, and compartmentalization into plastids or other membrane-rich organelles (Kaldorf et al., 1999; 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 tolerances to metals. Optimizing the use of arbuscular mycorrhizal fungi to permit growth of plants in soils contaminated with metals may require careful selection of specific fungal and host plant combinations for a given set of soil conditions. It will also likely require skillful use of inorganic and organic amendments to maximize plant growth and to capitalize on interactions or competitions between metals and elements such as P and sulfur, whose uptake is generally enhanced in mycorrhizal plants. For example, increased P may increase plant biomass and thus perhaps detoxify the potential effects of metals by dilution, precipitation or adsorption of metals onto polyphosphate granules. The non-target ecological effects of plants or fungi which have adsorbed, translocated and sequestered metals also need to be considered in parallel with efforts to revegetate soils contaminated with high levels of metals. Efforts to phytoremediate, reclaim or restore vegetation to soils contaminated with metals by use of mycorrhizal plant species and inocula is gaining acceptance. The literature indicates that one should also evaluate the potential effects on aboveground and belowground, invertebrate and vertebrate consumers of both plant and fungal tissues; the structure of the soil food; and plant community composition in surrounding areas (Kahn et al., 2000; Chaudhry et al., 1998; Entry et al., 1996b).

Propagating cultures of arbuscular mycorrhizal fungi in the absence of a host plant remains elusive. Research on methods to grow and characterize, develop and screen large numbers of arbuscular mycorrhizal fungi for tolerance to metals and toxic organic pollutants will continue to be hampered unless methods to grow these fungi in culture are further developed. The lack of correlation between colonization rates and a beneficial or detrimental host response perhaps suggests the need to look more closely at the diversity and competition among arbuscular mycorrhizal fungi colonizing roots. Identifying and culturing the most effective isolates could then be undertaken to select or develop genetically-improved strains customized for a particular set of soil conditions or host plants.

3.3. Toxic organic pollutants

3.3.1. Pesticides

Research involving the interaction of toxic organic pollutants, including pesticides, with arbuscular mycorrhizas has been largely limited to assessing effects of fungicides on mycorrhizal formation and P uptake. Interaction of multiple fungicides on the function of mycorrhizas is important in the context of minimizing effects of plant pathogens while maximizing beneficial effects of mycorrhizas to plant nutrition (Abd-Alla et al., 2000; Sukarno et al., 1996). Several studies have found that benomyl inhibits arbuscular mycorrhizal infection and P uptake in crop plants. Sukarno et al. (1996) reported that 31 mg benomyl kg^{-1} soil (manufacturer's recommended rate) reduced *Glomus* sp. formation on onion (*Allium cepa* L.) and P acquisition. However, Larsen et al. (1996) reported that 10 mg benomyl kg^{-1} soil reduced formation of mycorrhizas by *G. caledonium* on *Cucumis sativus* L. Merryweather and Fitter (1996) found that 63 mg benomyl kg^{-1} inhibited arbuscular mycorrhizal colonization on *Hyacinthoides non-scripta* L. Chouard ex. Roth. (bluebell). When mycorrhizal formation was reduced, these studies found that P uptake was also reduced. Several other studies also showed that benomyl reduced mycorrhizal formation in annual grasses leading to reduced plant biomass, but, P acquisition was not affected (Carey et al., 1992; West et al., 1993; Newsham et al., 1994).

Fumigation of soil with methyl bromide inhibits arbuscular mycorrhizal formation and P uptake by all plants that have been studied. Jawson et al. (1993) reported that soil fumigation with methyl bromide substantially reduced mycorrhizal formation on corn roots to a depth of 15 cm; below 15 cm roots became mycorrhizal. Afek et al. (1991) found that fumigation of soil with methyl bromide inhibited mycorrhizal formation in cotton, onion and pepper (*Capsicum annuum* L.). However, if soil was inoculated with *G. intraradices* spores after fumigation, these plants had higher rates of colonization by mycorrhizal fungi and greater plant biomass. Buttery et al. (1988) also found that methyl bromide fumigation of soil reduced mycorrhizal formation on, and P uptake by, peas (*Phaseolus vulgaris* L.) and soybean (*Glycine max* L.). Hass et al. (1987) reported that methyl bromide fumigation inhibited mycorrhizal formation on pepper. Menge (1982) and Brown et al. (1974) reported that methyl bromide fumigation inhibited mycorrhizal formation on, and P uptake by, wheat (*Triticus aesivium* L.) and potatoes (*Solanum tuberosum* L.). Sukarno et al. (1996, 1993), Despatie et al. (1989), Jabaji-Hare and Kendrick (1985, 1987) and Clark (1978) all reported that application of fosetyl-Al (aliette) reduced root growth, but stimulated mycorrhizal formation on, and P uptake by, several crop plants. However, application of approximately 13 mg ridomil kg^{-1} soil did not reduce colonization by *Glomus* sp. on onion roots (Sukarno et al., 1996).

3.3.2. Polychlorinated aliphatic and phenolic compounds

Arbuscular mycorrhizal plants to have been investigated to improve remediation of soils contaminated with chlorinated phenolic compounds, such as chloroacetamide herbicides (Hoagland et al., 1997), the deicing agent ethylene glycol (Rice et al., 1997), trichloroethylene (Gordon et al., 1997), polyaromatic hydrocarbons (Binet et al., 2000; Leyval and Binet, 1998; Qiu et al., 1997) and chlorinated phenols (Ensley et al., 1997). However, few studies examined explicitly the ability of arbuscular mycorrhizal fungi to degrade these chemicals, or the role of carbon allocation to the mycorrhizal fungus during the degradation process (Binet et al., 2000; Olexa et al., 2000; Leyval and Binet, 1998; Donnelly and Fletcher, 1994; Donnelly et al., 1994).

Vast expanses of land have been contaminated by various types of organic pollutants and metals. Current approaches to remediate these soils involves removing the soil from the site and treating it with various dispersing and chelating chemicals. Excavating and transporting this soil requires equipment, energy, and considerable amounts of personnel time, and is therefore expensive. These activities may also result in additional dispersal of the pollutants due to accidents occurring during the clean-up procedures (Entry et al., 1996b). As the costs to clean these sites is oftentimes prohibitive, few sites have actually been cleaned up. In contrast, phytoremediation not only may remediate a site but may also eventually reclaim it by fostering the establishment of a plant community. Phytoremediation of soil contaminated with organic pollutants is an emerging science and one in which mycorrhizas are of crucial importance. Evidence from Olexa et al. (2000) and Donnelly and Fletcher (1994) suggests that arbuscular mycorrhizal plants usually increase degradation of chlorinated phenolic compounds in soil. If phytoremediation of soils contaminated with chlorinated phenolic compounds is to become a feasible and cost effective management option, research on the efficacy of mycorrhizal plants to enhance degradation of these compounds in situ is necessary.

4. Conclusions

Arbuscular mycorrhizal fungi are of interest for their reported roles in alleviating a diverse array of soil-associated plant stresses. The majority of research on the role of mycorrhizas to modify effects of stresses has focused on mycorrhizal formation and nutrient acquisition under extreme changes in water amounts, temperature, pH and inorganic nutrient availability. There has been increased interest in the role of soil quality and its influence on the sustainability and resiliency of both agricultural and forest ecosystems. However, there is a paucity of research on this general topic considering the roles of arbuscular mycorrhizal fungi. Arbuscular mycorrhizas have the ability to alleviate many anthropogenic stresses, including effects of metals and polychlorinated aliphatic and phenolic pollutants. Remediation of soils contaminated with toxic pollutants using specific combinations of plants and species or strains of mycorrhizal fungi deserves increased emphasis. Before the benefits of using arbuscular mycorrhizal plants to improve soils with adverse physical and chemical conditions can be fully realized, research is needed to improve our ability to successfully culture arbuscular mycorrhizal fungi, to increase our understanding of the genetic diversity of these organisms, and to assess the range of physiological capabilities of these ubiquitous symbionts.

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