Symbiosis, 14 (1992) 413–425
Balaban, Philadelphia/Rehovot

Review article

Mycorrhizae in the Agricultural Plant-Soil System

GABOR J. BETHLENFALVAY
Horticultural Crops Research Laboratory, U.S. Department of Agriculture
Agricultural Research Service, Corvallis, Oregon 97330, USA
Tel. (503) 750 8785, Telex (503) 750 8764

Received November 20, 1991; Accepted March 3, 1992

Abstract

Vesicular-arbuscular mycorrhizal (VAM) fungi and their host plants evolved together under diverse edaphic and environmental conditions. They are interdependent and contribute to stability in plant communities. Soils typically contain several species of VAM fungi, all of which may colonize the roots of most crop plants. However, the fungi may differ in their ability to elicit specific host-plant or host-soil responses, suggesting that a combination of fungi is needed to function as an adequate plant-soil interface. Since in agricultural ecosystems the introduction of exotic weeds and crops, cultivation, and chemicals alter the composition and vitality of the VAM mycoflora, management practices enhancing the combined effects of surviving and introduced VAM fungi must be developed. Benefits of introduction depend on the potential of VAM fungi to exploit soil resources and to tolerate the natural and culturally imposed conditions of a host soil, and on their compatibility with specific host plants in forming associations of improved productivity. Fungi must therefore be selected to satisfy the requirements of the agricultural situations whose problems they are intended to alleviate. In addition to applications in plant nutrition, VAM fungi are involved in crop rotation, intercrops, grazing, and weed and pest control. Perhaps the greatest potential for the utilization of VAM fungi in sustainable plant production systems lies in the improvement of soil stability and erosion control.

Keywords: biocide, crop productivity, cropping systems, soil aggregation, vesicular-arbuscular mycorrhizal fungi

0334-5114/92 /$03.50

1. Mycorrhizae and the Ecology of Agricultural Systems

The productivity of agricultural systems is influenced by environmental stresses and stresses resulting from the cultural practices employed by man. The latter is of particular interest in sustainable agriculture, because the transition to sustainability is advanced by an understanding of the consequences of practices under our control. This change is not unlike the processes leading to stabilization in natural ecosystems that were described by Odum in his *Strategy of Ecosystem Development*: "an understanding of ecological succession provides a basis for resolving man's conflict with nature" (Odum, 1969).

The symbiotic VAM fungi (Morton and Benny, 1990) that colonize the roots and soils of crop and weed plants (Hayman, 1982, Trappe, 1987) form part of this understanding since they have a major impact on the functioning and stability of any ecosystem. They are an important group of soil-borne microorganisms that contribute substantially to the productivity and longevity of man-made ecosystems (Harley and Smith, 1983). In a sustainable agricultural system characterized by low levels of disturbance, the significance of mycorrhizae (Pankow et al., 1991) will be similar to that in natural ecosystems at advanced successional stages. In such systems the role of mycorrhizae may be expressed not only by the acquisition of nutrients by one host plant, but also by a redistribution of nutrients between many host plants and between host plants and host soils.

2. Mycorrhize Interact With Soil Factors

Emphasis by today's intensive agriculture is on maximum production of commodities for consumption (CAST, 1982). This approach has traditionally resulted in germplasm selection favoring translocation of carbon compounds to portions of crop plants of immediate economic interest. It is well-known that a proper allocation of carbon to the roots is needed to preserve soil structure and to insure subsequent harvests (Boyle et al., 1989). Yet, prevailing practices continue to be detrimental to sustainable agriculture and result in erosion and desertification (CAST, 1982, 1988; Larson, 1986).

The process of carbon allocation from plant to soil and its role in soil structure formation have been of interest throughout this century (Harris et al., 1966; Emerson et al., 1986). The Concept of the plant and soil as one system is not new (Devaux, 1904). It has been supported by research on soils at all levels, from the molecular and ionic aspects (Jenny and Grossenbacher, 1963) to those involving soil microbiology in soil aggregate formation (Tisdall and Oades, 1982). but ecologists are only beginning to realize the importance of soil structure in the control of many below-ground processes (Jastrow and Miller, 1991). The flow of carbon to roots and to its associated microorganisms may seem wasteful in commercial terms, but in ecological terms it enables plants to grow where they otherwise could not (Lynch and Whipps, 1990).

When the general loss of carbon from the plant (its transfer to the soil) is mediated primarily by exudation, the population density of soil microbiota falls off steeply with increasing distance from the root. As a result, the plant's direct sphere of influence on soil biology was thought to be concentrated in the narrow zone ($\approx$ 2 mm) of the rhizosphere (Newman and Watson, 1977; Rovira, 1969). When considering other mechanisms of carbon transfer, such as fungal hyphae, these narrow limits are expanded considerably (Gardner et al., 1983). Soil mycelia of VAM fungi, in particular, not only influence the flow rate and composition of root exudates, but contain a substantial portion of root-derived carbon in the soil (Jakobsen and Rosendahl, 1990). This fungal biomass is also available as a substrate to microbial metabolism. Since VAM hyphae can penetrate in excess of 9 cm of root-free soil (Camel et al., 1991), their effect on aggregate-forming activities of the mycorrhizosphere biota of the bulk soil is of particular interest (Linderman, 1988).

Aggregate size and stability are dynamic soil properties which change in response to aggregating and disaggregating forces, such as temperature, moisture and microbial activity (Gish and Browning, 1948). One of these forces is the cropping system itself: aggregate stability of soils improves after certain crops, but deteriorates after others (Reid and Goss, 1981). This effect has been related to the differing capacities and species and cultivars to transport carbon to the rhizosphere (Liljeroth et al., 1990), but is complicated by differences in the capability of exudates produced by different plants to stabilize the soil (Pojasok and Kay, 1990). Indeed, the influence of major crops, such as soybean (*Glycine max* (L.) Merr.) and corn (*Zea mays* L.), on aggregate stability result in different levels of soil loss. Because of their inconsistency, such relative effects are usually ascribed to the great variety of climatic, soil, cropping, and tillage factors present in the field (Alberts and Wendt, 1985). Currently, however, Johnson et al. (1991a) have shown that cropping history (corn-soybean rotation) has a marked effect on the size and composition of the VAM mycoflora. These authors have not related soil aggregation with changes in VAM fungal populations in response to crop rotation. Yet, their data are clearly relevant to the soil-loss phenomenon in the light of Jakobsen and Rosendahl's (1990) findings on VAM effects on carbon flow into the soil.

Studies on rhizodeposition, or loss of carbon from the roots, which provides the substrates for soil microbial activity (Whipps and Lynch, 1985), have not yet considered VAM fungi as a factor (Jakobsen and Rosendahl, 1990), even though VAM mycelia may represent the largest fraction of soil biomass (Hayman, 1978) and may reach up to 20% of the total dry mass of the mycorrhiza (Bethlenfalvay et al., 1982). Correlations between soil structural parameters and the pool of organic matter resulting from rhizodeposition are often inconsistent, suggesting differences in the effectiveness of some components of the pool as agents for stabilizing aggregates (Perfect and Kay, 1990). The nature and relative amounts of these components, filamentous structures (hyphae and root hairs) or plant or fungal mucigels, is likely to have different effects on the cementing of soil particles; effects that may be interpreted differently depending on the investigative approach employed (Burns and Davies, 1986). The suggestion of these authors that filamentous structures and mucilages are involved in different stages in water-stable aggregate formation and stabilization could explain the synergistic effects on soil aggregation produced by the mycorrhiza (fungus-root), compared to individual component (root or fungus alone) effects (R.S. Thomas, unpublished data).

3. Mycorrhizae Interact With Cultural Practices

Most aspects of cultural stress have deleterious effects on mycorrhiza formation or on the survival and abundance of the propagules of VAM fungi in the soil. The degree of impoverishment or disappearance of the VAM mycoflora is an indicator for the decrease in the stability of the plant-soil system, just as the level of cultural stress is a measure of sustainability of agriculture.

Soil disturbance affects root and soil colonization by VAM fungi (Abbott and Robson, 1991), showing a relationship between the formation of VAM mycelia in the root (Evans and Miller, 1990) and in the soil (McGonigle et al., 1990). The disruption of mycorrhiza formation by soil disturbance results in decreased phosphorus uptake by plants (Evans and Miller, 1988; Fairchild and Miller, 1988). Tillage effects on plant phosphorus nutrition had been noted previously, (Anderson et al., 1987, Mulligan et al., 1985; O'Halloran et al., 1986), and were also linked to VAM development. Disturbance effects vary with soils and vegetation, and affect the density of infective propagules needed to reestablish VAM colonization differently (Jasper et al., 1991).

Fallowing (Fixen et al., 1984), like soil disturbance, is a form of stress that relates mycorrhiza formation to plant nutrient deficiency. VAM colonization and propagule densities decline as a result of fallowing, Harinikumar and Bagyaraj (1988), and result in plant deficiencies in phosphorus and zinc (Thompson, 1987; Thompson et al., 1986). This process is related to an increased susceptibility of roots to infection by pathogens, suggesting that VAM fungi may protect roots from infection (Thompson and Wildermuth, 1988). This effect may be partly due to nutrient deficiency, but it is an example of the complexity of the involvement of VAM funi with plant productivity and stress. To reestablish VAM propagules after a prolonged absence of host plants without a marked loss in productivity, Thompson (1988) proposed that plants of low VAM dependency and high root density be grown first after a long fallow period.

Crop rotation benefits plant health and growth, but the exact reason for the yield response to rotation is not well-known (Crookston et al., 1988 and 1991). Clearly, improved understanding of the causes could improve management techniques. The involvement of mycorrhizae in growth problems associated with tillage and rotation (Vivekanandan and Fixen, 1991) was known since Stremska's (1975) report on interactions between mycorrhizae, nitrogen fertilization, and cropping-systems. Enhanced VAM colonization and spore production as a result of rotation were demonstrated in a number of cropping sequences (Baltruschat and Dehne, 1989; Dodd et al., 1990; Sieverding and Leihner, 1984a), while rotation, or monoculture, with nonVAM hosts were inhibitory (Baltruschat and Dehne, 1988; Kruckelmann, 1975). Rotation sequences may also influence the species composition of the VAM mycoflora growing with different crop plants (Johnson et al., 1991a and 1991b). It was suggested that yield decline associated with continuous cropping may be due to VAM-fungal proliferation and a resulting parasitic reduction of host-plant growth (Johnson et al., 1992). The formation of the distinct fungal communities in soils with different cropping histories was ascribed to the host plant and to the edaphic changes in soils mediated by plants as a result of continuous monoculture (Johnson et al., 1991b). A better understanding of rotation effects would help in selecting more effective VAM fungi for use in agriculture.

In intercrop systems, such as legume-cereal associations (Haynes, 1980), mutual enhancement by the associated plans is often observed. The hyphae of VAM fungi colonize and connect the roots of adjacent plants (Francis and Read, 1984; Ritz and Newman, 1984; van Kessel et al., 1985). It had been suggested that VAM fungi are involved in a transfer and distribution of nutrients in such plant communities (Read et al., 1985), but important changes in plant growth or nutrition have not yet been demonstrated due to direct, mycorrhiza-mediated nutrient transfer between plants (Hamel et al., 1991; Newman, 1988). Legume effects on grasses are variable and can range from yield enhancement (Crookston and Hill, 1979) to yield decline (Hall, 1978). Nitrogen input into the intercrop system by legumes is often a function of phosphorus availability (Voss and Schrader, 1984), which is importantly influenced by VAM fungi (Bethlenfalvay et al., 1991, Hamel and Smith, 1991). To utilize VAM fungi in intercrops more effectively, compatibility among the symbionts and the timing of periods of peak sink demand by the associated plans will have to be known.

Shoot removal (grazing, mowing) from plants affects the entire plant-soil system with little-known effects. Grazing may increase (Wallace, 1987a) or decrease (Trent et al., 1988; Bethlenfalvay and Dakessian, 1984) VAM colonization, or leave it unaffected (Wallace, 1987b). Mycorrhiza formation may also depend on grazing intensity (Bethlenfalvay et al., 1985). The densities of VAM spores in the soil also depend on grazing effects on the host plant (Bethlenfalvay et al., 1985; Wallace, 1987a). More information is needed to resolve these contradictions. Factors that affect the problem are: (1) the capability of the host plant to provide the symbionts (including the soil biota) with photosynthetic products (Bayne et al., 1984), and the dependency of the host on its VAM endophytes (Hetrick et al., 1987); (2) the timing, intensity, and duration of shoot removal in conjunction with seasonal variations in mycorrhiza formation (Bethlenfalvay et al., 1985; Cade-Menun et al., 1991); (3) the effects of carbon loss on host-soil stability (Jakobsen and Rosendahl, 1990; Lynch and Bragg, 1985); and (4) proper, standardized methods of evaluation (McNaughton and Oesterheld, 1990), which would permit workers to compare results.

Costs and benefits to plants of maintaining mycorrhizae under photosynthesis stress have been compared by Fitter (1991). An assessment of the VAM soil mycelium is of particular importance when the host is under carbon stress. The development of VAM soil hyphae is strongly influenced by soil nutrient availability (Miller, 1987). The hyphae also facilitate the flow of carbon compounds to the bulk soil (Jakobsen and Rosendahl, 1990), which depends on this process for its stability. The relationship between hyphal development and plant/soil nutrient ratios suggests a role for mycorrhizae in stabilizing ecosystem nutrient fluxes and for maintaining plant nutrient levels within narrow ranges compared with soil variation (McNaughton and Oesterheld, 1990).

4. Mycorhizae Interact With Agro-Chemicals

Concern over the deterioration of the natural resource base in U.S. agriculture (CAST, 1988) resulted in a renewed interest in conservation tillage (Larson and Osborne, 1982). Reduced tillage is successful in controlling erosion, but it necessitates increased biocide use to control crop loss (Phillips et al., 1980). However, the impact of biocides on the environment and human health (CAST, 1988) is also a matter of grave concern. Agricultural chemicals are successful in controlling pests and pathogens, but their application often also results in the indiscriminate killing of beneficial microorganisms (Domsch, 1964), such as VAM fungi. The literature of VAM-biocide interactions have been reviewed by Vyas (1988) and Trappe et al. (1984).

VAM fungi are integral parts of both the plant (Gianinazzi et al., 1982) and of the population of soil microbes (Linderman, 1991). Biocides may therefore affect VAM fungi directly or indirectly through their effects on the host plant or on the host-soil biota (Garcia-Romera, 1988; Trappe et al., 1984). These complex interactions are of particular interest in sustainable agriculture, since biocide-induced retardation of VAM-hyphal growth, the inhibition of root colonization, and a shift in species combinations in the soil can be important for soil stability and plant production (Dehn et al., 1990; Sieverding and Leihner, 1984b).

Biocide treatments have varied effects on mycorrhizae. They may enhance as well as inhibit VAM colonization and sporulation (Vyas, 1988). Fungicides may also improve mycorrhiza formation by controlling hyperparasites (Atilano and van Gundy, 1979), and VAM fungi, in turn, may improve host-plant resistance to pesticide stress (Menge, 1982; Ocmpo and Barea, 1985; Siqueira et al., 1991). Utilization of biocides based on a knowledge of their effects on VAM fungi, in addition to that on pathogens and pests, is of practical significance in view of the potential of VAM fungi as biocontrol agents (Caron, 1988; Schönbeck, 1987).

5. Conclusions

The fungi of the mycorrhizal symbiosis are crucial components of both plant and soil development and health. As agents of plant productivity and soil conservation, they have a useful role to play in agriculture. At present, we do not have enough information on the effects of specific VAM-fungal isolates on specific plant or soil problems. This information will have to be obtained before VAM fungi can be fully integrated into agricultural practice as a management tool. Research on the VAM plant-soil system is needed on many fronts to achieve this goal: (1) elucidation of the conditions for large-scale production of host-free inocula; (2) selection of effective isolates from naturally occurring populations or by artificial, directional selection methods; and (3) identification of specific cultural and environmental conditions which can be alleviated by mycorrhizae. Finally, we should provide the user in the field with specific product-use recommendations.

REFERENCES

Abbott, L.K., and Robson, A.D. 1991. Field management of VA mycorrhizal fungi. In: *The Rhizosphere and Plant Growth.* D.L. Keister and P.B. Cregan, eds. Kluwer Academic Publishers, Dordrecht, pp. 355–362.

Alberts, E.E. and Wendt, R.C. 1985. Influence of soybean and corn cropping on soil aggregate size and stability. *Soil Sci. Soc. Am. J.* **49:** 1534–1537.

Anderson, E.L., Millner, P.D., and Kunishi, H.M. 1987. Maize root length density and mycorrhizal infection as influenced by tillage and soil phosphorus. *J. Plant Nutr.* **10:** 1349–1356.

Atilano, R.A. and van Gundi, M.H. 1979. Effects of some systemic, nonfumigant and fumigant nematicides on grape mycorrhizal funi and citrus nematode. *Plant Dis. Rep.* **63:** 729–731.

Baltruschat, H. and Dehne, H.W. 1988. The occurrence of vesicular-arbuscular mycorrhiza in agro-ecosystems. I. Influence of nitrogen fertilization and green manure in continuous monoculture and in crop rotation on the inoculum potential of winter wheat. *Plant Soil* **107:** 279–284.

Baltruschat, H. and Dehne, H.W. 1989. The occurrence of vesicular-arbuscular mycorrhiza in agro-ecosystems. II. Influence of nitrogen fertilization and green manure incontinuous monoculture and in crop rotation on the inoculum potential of winter barley. *Plant Soil* **113:** 251–256.

Bayne, H.G., Brown, M.S., and Bethlenfalvay, G.J. 1984. Defoliation effects on mycorrhizal colonization, nitrogen fixation and photosynthesis in the *Glycine-Glomus-Rhizobium* symbiosis. *Physiol. Plant.* **62:** 576–580.

Bethlenfalvay, G.J. and Dakessian, S.1984. Grazing effects on mycorrhizal colonization and floristic composition of the vegetation on a semiarid range in northern Nevada. *J. Range Manage.* **37:** 312–316.

Bethlenfalvay, G.J., Evans, R.A., and Lesperance, A.L. 1985. Mycorrhizal colonization of crested wheatgrass as influenced by grazing. *Agron. J.* **77:** 233–236.

Bethlenfalvay, G.J., Pacovsky, R.S., and Brown, M.S. 1982. Parasitic and mutualitic associations between a mycorrhizal fungus and soybean: development of the endophyte. *Phytopathology* **72:** 894–897.

Bethlenfalvay, G.J., Reyes-Solis, M.G., Camel, S.B., and Ferrera-Cerrato, R. 1991. Nutrient transfer between the root zones of soybean and maize plants connected by a common mycorrhizal inoculum. *Physiol. Plant.* **82:** 423–432.

Boyle, M., Frankenberger, W.T., and Stolzy, L.H. 1989. The influence of organic matter on soil aggregation and water infiltration. *J. Prod. Agric.* **2:** 290–299.

Burns, R.G. and Davies, J.A. 1986. The microbiology of soil structure. *Biol. Agric. Hortic.* **3:** 95–113.

Cade-Menun, B.J., Berch, S.M., and Bomke, A.A. 1991. Seasonal colonization of winter wheat in South Coastal British Columbia by vesicular-arbuscular mycorrhizal fungi. *Can. J. Bot.* **69:** 78–86.

Camel, S.B., Reyes-Solis, M.G., Ferrera-Cerrato, R., Franson, R.L., Brown, M.S., and Bethlenfalvay, G.J. 1991. The growth of mycorrhizal mycelia through bulk soil. *Soil Sci. Soc. Am. J.* **58:** 389–393.

Caron, M. 1989. Potential use of mycorrhizae in control of soil-borne diseases. *Can. J. Plant Pathol.* **11:** 177–179.

CAST (Council for Agricultural Science and Technology). 1982. *Soil Erosion: Its Agricultural, Environmental, and Socio-Economic Implications.* CAST Rep. 92, ISSN 0194-4088, Ames, Iowa.

CAST (Council for Agricultural Science and Technology). 1988. *Long-Term Viability of U.S. Agriculture.* CAST Rep. 114, ISSN 0194-4088, Ames, Iowa..

Crookston, R.K. and Hill, D.S. 1979. Grain yields and land equivalent ratios from intercropping corn and soybean in Minnesota. *Agron. J.* **71:** 41–44.

Crookston, R.K., Kurle, J.E., Copeland, P.B., Ford, J.H., and Lueschen, W.E. 1991. Rotational cropping sequence affects yield of corn and soybean. *Agron. J.* **83:** 108–113.

Crookston, R.K., Kurle, J.E., and Lueschen, W.E. 1988. Relative ability of soybean, fallow, and triacontanol to alleviate yield reductions associated with growing corn continuously. *Crop Sci.* **28:** 145–147.

Dehn, B., Bodmer, M., and Schüepp, H. 1990. Influence of herbicides on VA mycorrhizal propagation in soil. *Symbiosis* **9:** 223–227.

Devaux, M.H. 1904. Comparaison des pouvoirs absorbants des parois cellulaires et du sol pour les sels dissous. *P.V. Soc. Sci. Bordeaux Proc.* **1904:** 32–38.

Dodd, J.C., Arias, I., Koomen, I., and Hayman, D.S. 1990. The management of populations of vesicular-arbuscular mycorrhizal fungi in acid-infertile soils of a savanna ecosystem. *Plant Soil* **122:** 229–240.

Domsch, K.H. 1964. Soil fungicides. *Annu. Rev. Phytopathol.* **2:** 293–320.

Emerson, W.W., Foster, R.C., and Oades, J.M. 1986. Organo-mineral complexes in relation to soil aggregation and structure. In: *Interactions of Soil Minerals with Natural Organics and Microbes.* P.M. Huang and M. Schnitzer, eds. SSSA Spec. Pub. 17, ASA, CSSA and SSSA, Madison.

Evans, D.G. and Miller, M.H. 1988. Vesicular-arbuscular mycorrhiza and the soil-disturbance-induced reduction of nutrient absorption in maize. I. Causal relations. *New Phytol.* **110:** 67–74.

Evans, D.G. and Miller, M.H. 1990. The role of the external mycelial network in the effect of soil disturbance upon vesicular-arbuscular mycorrhizal colonization of maize. *New Phytol.* **114:** 65–71.

Fairchild, G.L. and Miller, M.H. 1988. Vesicular-arbuscular mycorrhizas and the soil-disturbance-induced reduction of nutrient absorption in maize. II. Development of the effect. *New Phytol.* **110:** 75–84.

Fitter, A.H. 1991. Costs and benefits of mycorrhizas: Implications for functioning under natural conditions. *Experientia* **47:** 350–355.

Fixen, P.E., Gerwing, J.R., and Farber, B.G. 1984. Phosphorus requirements of corn and soybeans following fallow. In: *Southeastern Farm Report.* Agric. Exp. Stn., Dept. of Plant Science, South Dakota State Univ., Brookings, SD, pp. 72–80.

Francis, R.A. and Reed, D.J. 1984. Direct transfer of carbon between plants connected by vesicular-arbuscular mycorrhizal mycelium. *Nature* **307:** 53–56.

Garcia-Romera, I. and Ocampo, J.A. 1988. Effect of the herbicide MCPA on VA mycorrhizal infection and growth of *Pisum sativum*. *Z. Planzenernähr. Bodenk.* **151:** 225–228.

Gardner, W.K., Parbery, D.J., Barber, D.A., and Swinden, L. 1983. The acquisition of phosphorus by *Lupinus albus* L. V. The diffusion of exudates away from roots: a computer simulation. *Plant Soil* **72:** 13–29.

Gianinazzi, S., Gianinazzi-Pearson, V., and Trouvelot, A., eds. 1982. Les mycorrhizes, partie intégrante de la plante: biologie et perspectives d'utilization. Les Colloques d'INRA, No. 13, Paris, 395 pp.

Gish, R.E. and Browning, G.M. 1948. Factors affecting the stability of soil aggregates. *Soil Sci. Soc. Am. Proc.* **13:** 51–55.

Hall, I.R. 1978. Effects of endomycorrhizas on the competitive ability of white clover. *N.Z. J. Agric. Res.* **21:** 509–515.

Hamel, C., Furlan, V., and Smith, D.L. 1991. N_2 fixation and transfer in a field-grown mycorrhizal corn and soybean intercrop. *Plant Soil* **133:** 177–185.

Hamel, C. and Smith, D.L. 1991. Interspecific N transfer and plant development in a mycorrhizal field-grown mixture. *Soil Biol. Biochem.* **23:** 661–665.

Harinikumar, K.M. and Bagyaraj, D.J. 1988. Effect of crop rotation on native vesicular-arbuscular mycorrhizal propagules in soil. *Plant Soil* **110:** 77–80.

Harley, J.L. and Smith, S.E. 1983. *Mycorrhizal Symbiosis.* Academic Press, New York.

Harris, R.F., Chesters, G., and Allen, O.N. 1966. Dynamics of soil aggregation. *Adv. Agron.* **18:** 107–169.

Hayman, D.S. 1978. Endomycorrhizas. In: *Interactions Between Non-pathogenic Micro-organisms and Plants.* Y.R. Dommergues and S.V. Krupa, eds. Elsevier, Amsterdam, pp. 401–442.

Hayman, D.S. 1982. Influence of soils and fertility on activity and survival of vesicular-arbuscular mycorrhizal fungi. *Phytopathology* **72:** 1119–1125.

Haynes, R.J. 1980. Competitive aspects of the grass-legume association. *Adv. Agron.* **33:** 227–261.

Hetrick, B.A.D., Kitt, D.G., and Wilson, G.T. 1987. Mycorrhizal dependence and growth habit of warm-season and cool-season tallgrass prairie plants. *Can. J. Bot.* **66:** 1376–1380.

Jakobsen, I. and Rosendahl, L. 1990. Carbon flow into soil and external hyphae from roots of mycorrhizal cucumber plants. *New Phytol.* **115:** 77–83.

Jasper, D.A., Abbott, L.K., and Robson, A.D. 1991. The effects of soil disturbance on vesicular-arbuscular mycorrhizal fungi in soils from different vegetation types. *New Phytol.* **118:** 471–476.

Jastrow, J.D. and Miller, R.H. 1991. Methods for assessing the effects of biota on soil structure. *Agric. Ecosystems Environ.* **34:** 279–303.

Jenny, H. and Grossenbacher, K. 1969. Root-soil boundary zones as seen in the electron microscope. *Soil Sci. Soc. Am. Proc.* **27:** 273–277.

Johnson, N.C., Copeland, P.J., Crookston, R.K., and Pfleger, F.L. 1992. Mycorrhizae: A possible explanation for yield decline associated with continuous cropping of corn and soybean. *Agron. J.* (in press).

Johnson, N.C., Pfleger, F.L., Crookston, R.K., Simmons, S.R., and Copeland, P.J. 1991a. Vesicular-arbuscular mycorrhizas respond to corn and soybean cropping history. *New Phytol.* **117:** 657–663.

Johnson, N.C., Zak, D.R., Tilman, D., and Pfleger, F.L. 1991b. Dynamics of vesicular-arbuscular mycorrhizae during old-field succession. *Oecologia* **86:** 349–358.

Kruckelmann, H.W. 1975. Effects of fertilizers, soils, soil tillage, and plant species on the frequency of Endogone chlamydospores and mycorrhizal infection in arable soils. In: *Endomycorrhiza.* F.E. Sanders, B. Mosse, and P.B. Tinker, eds. Academic Press, New York, pp. 511–525.

Larson, W.E. 1986. The adequacy of world soil resources. *Agron. J.* **78:** 221–225.

Larson, W.E. and Osborne, G.J. 1982. Tillage accomplishments and potential. In: *Predicting Tillage Effects on Soil Physical Properties and Responses.* P.W. Unger and D.M. van Doren, eds. Spec. Pub. 44, American Society of Agronomy, Madison, pp. 1–11.

Liljeroth, E., Van Veen, J.A., and Miller, H.J. 1990. Assimilate translocation to the rhizosphere of two wheat lines and subsequent utilization by rhizosphere microorganisms at two soil nitrogen concentrations. *Soil Biol. Biochem.* **22:** 1015–1021.

Linderman, R.G. 1988. Mycorrhizal interactions with the rhizosphere microflora: the mycorrhizosphere effect. *Phytopathology* **78:** 366–371.

Linderman, R.G. 1991. Mycorrhizal interactions in the rhizosphere. In: *The Rhizosphere and Plant Growth.* D.L. Keister and P.B. Cregan, eds. Kluwer Academic Publishers, Dordrecht, pp. 343–348.

Lynch, J.M. and Bragg, E. 1985. Microorganisms and soil aggregate stability. *Adv. Soil Sci.* **2:** 133–171.

Lynch, J.M. and Whipps, J.M. 1991. Substrate flow in the rhizosphere. *Plant Soil* **129:** 1–10.

McGonigle, T.P., Evans, D.G., and Miller, M.H. 1990. Effect of degree of soil disturbance on mycorrhizal colonization and phosphorus absorption by maize in growth chamber and field experiments. *New Phytol.* **116:** 629–636.

McNaughton, S.J. and Oesterheld, M. 1990. Extramatrical mycorrhizal abundance and grass nutrition in a tropical grazing ecosystem, the Serengeti National Park, Tanzania. *Oikos* **59:** 92–96.

Menge, J.A., Jarrell, W.M., Labanauskas, C.K., Ojala, J.C., Huszar, C., Johnson, E.L.V., and Sibert, D. 1982. Predicting mycorrhizal dependency of Troyer citrange on *Glomus fasciculatus* in California citrus soils and nursery mixes. *Soil Sci. Soc. Am. J.* **46:** 762–768.

Miller, R.M. 1987. The ecology of vesicular-arbuscular mycorrhizae in grass- and shrublands. In: *Ecophysiology of VA Mycorrhizal Plants.* G.R. Safir, ed. CRC Press, Inc., Boca Raton, FL, pp. 135–170.

Morton, J.B. and Benny, G.L. 1990. Revised classification of arbuscular mycorrhizal fungi (Zygomycetes): a new order, Glomales, two new Acaulasporaceae and Gigasporaceae, with an emendation of Glomaceae. *Mycotaxon* **37:** 471–491.

Mulligan, M.F., Smucker, A.J.M., and Safir, G.F. 1985. Tillage modification of dry edible bean root colonization by VAM fungi. *Agron. J.* **77:** 140–144.

Newman, E.I. 1988. Mycorrhizal links between plants: Their functioning and ecological significance. *Adv. Ecol. Res.* **18:** 243–270.

Newman, E.I. and Watson, A. 1977. Microbial abundance in the rhizosphere – a computer model. *Plant Soil* **48:** 17–56.

Ocampo, J.A. and Barea, J.M. 1985. Effect of carbamate herbicides on VA mycorrhizal infection and plant growth. *Plant Soil* **85:** 375–383.

Odum, E.P. 1969. The strategy of ecosystem development. *Science* **164:** 262–270.

O'Halloran, I.P., Miller, M.H., and Arnold, G. 1986. Absorption of P by corn (*Zea mays* L.) as influenced by soil disturbance. *Can. J. Soil Sci.* **66:** 287–302.

Pankow, W., Boller, T., and Wiemken, A. 1991. The significance of mycorrhizas for protective ecosystems. *Experientia* **47:** 391–394.

Perfect, E. and Kay, B.D. 1990. Relations between aggregate stability and orgganic components for a silt loam soil. *Can. J. Soil Sci.* **70:** 731–735.

Phillips, R.E., Blevins, R.L., Thomas, G.W., Frye, W.W., and Phillips, S.H. 1980. No-till agriculture. *Science* **208:** 1108–1113.

Pojasok, T. and Kay, B.D. 1990. Effect of root exudates from corn and bromegrass on soil structural stability. *Can. J. Soil Sci.* **70:** 351–362.

Read, D.J., Francis, R., and Finlay, R.D. 1985. Mycorrhizal mycelia and nutrient cycling in plant communities. In: *Ecological Interactions in Soil.* A.H. Fitter, ed. Blackwell Scientific, Oxford, pp. 193–217.

Reid, J.B. and Goss, M.J. 1981. Effect of living roots of different plant species on the aggregate stability of two arable soils. *J. Soil Sci.* **32:** 521–541.

Ritz, K. and Newman, E.I. 1984. Movement of ^{32}P between intact grassland plants of the same age. *Oikos* **43:** 138–142.

Rovira, A.D. 1969. Plant root exudates. *Bot. Rev.* **35:** 35–57.

Schönbeck, F. 1979. Endomycorrhiza in relation to plant disease. In: *Soil-Born Plant Pathogens.* B. Schippers and W. Gams, eds. Academic Press, New York, pp. 271–292.

Sieverding, E. and Leihner, D.E. 1984a. Influence of crop rotation and intercropping of cassava with legumes on VA mycorrhizal symbiosis of cassava. *Plant Soil* **80:** 143–146.

Sieverding, E. and Leihner, D.E. 1984b. Effect of herbicides on population dynamics of VA-mycorrhiza with cassava. *Angew. Bot.* **58:**: 283–294.

Siqueira, J.O., Safir, G.R., and Nair, M.G. 1991. VA-mycorrhizae and mycorrhiza stimulating isoflavonoid compounds reduce plant herbicide injury. *Plant Soil* **134:** 233–242.

Stremska, J. 1975. Mycorrhiza in farm crops grown in monoculture. In: *Endomycorrhiza.* F.E. Sanders, B. Mosse and P.B. Tinker, eds. Academic Press, New York, pp. 527–535.

Thompson, J.P. 1987. Decline of vesicular-arbuscular mycorrhizae in long fallow disorder of field crops and its expression in phosphorus deficiency of sunflower. *Aust. J. Agric. Res.* **38:** 847–867.

Thompson, J.P., Clewett, T.J., Fiske, M.L., and Lister, P.E. 1986. Mycorrhiza research. Role of vesicular-arbuscular mycorrhiza (VAM) in long fallow disorder. Queensland Wheat Res. Inst. Biennial Rep. for 1982–1984. Queensland Dept. of Primary Industries, Toowoomba, Australia, pp. 35–36.

Thompson, J.P. and Wildermuth, G.B. 1988. Colonization of crop and pasture species with vesicular-arbuscular mycorrhizal fungi and a negative correlation with root infection by *Bipolaris sorokiniana*. *Can. J. Bot.* **69:** 687–693.

Tisdall, J.M. and Oades, J.M. 1982. Organic matter and water-stable aggregates in soils. *J. Soil Sci.* **33:** 141–163.

Trappe, J.M. 1987. Phylogenetic and ecologic aspects of mycotrophy in the angiosperms from an evolutionary standpoint. In: *Ecophysiology of VA Mycorrhizal Plants.* G.R. Safir, ed. CRC Press, Inc., Boca Raton, FL, pp. 5–25.

Trappe, J.M., Molina, R., and Castellano, M. 1984. Reactions of mycorrhizal fungi and mycorrhiza formation to pesticides. *Annu. Rev. Phytopathol.* **22:** 331–359.

Trent, J.D., Wallace, L.L., Svejcar, T.J., and Christensen, S. 1988. Effect of grazing on growth, carbohydrte pools, and mycorrhizae in winter wheat. *Can. J. Plant Sci.* **68:** 115–120.

van Kessel, C., Singleton, P.W., and Hoben, H.J. 1985. Enhanced N transfer from soybean to maize by vesicular-arbuscular mycorrhizal (VAM) fungi. *Plant Physiol.* **79:** 562–563.

Vivekanandan, M. and Fixen, P.E. 1991. Cropping systems effects on mycorrhizal colonization, early growth, and phosphorus uptake of corn. *Soil Sci. Soc. Am. J.* **55:** 136–140.

Voss, R.D. and Shrader, W.D. 1984. Rotation effects and legume sources of nitrogen for corn. In: *Organic Farming: Current Technology and its Role in a Sustainable Agriculture.* D.F. Bezdicek, J.F. Power, D.R. Keeney and M.J. Wright, eds. American Society of Agronomy, Spec. Pub. 16, Madison, pp. 61–68.

Vyas, S.C. 1988. Chapter 12: Mycorrhizae. *Nontarget Effects of Agricultural Fungicides.* CRC Press, Boca Raton, FL, pp. 169–184.

Wallace, L.L. 1987a. Effects of clipping and soil compaction on growth, morphology and mycorrhizal colonization of *Schizachyrium scoparium*, a C_4 bunchgrass. *Oecologia* **72:** 423–428.

Wallace, L.L. 1987b. Mycorrhizas in grasslands: Interactions of ungulates, fungi and drought. *New Phytol.* **105:** 619–632.

Whipps, J.M. and Lynch, J.M. 1985. Energy losses by the plant in rhizodeposition. *Ann. Proc. Phytochem. Soc. Eur.* **26:** 59–71.