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Mycorrhizal Ecology

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Introduction

Mycorrhizae are ubiquitous in terrestrial ecosystems. With an increasing awareness that this symbiotic association plays important roles in plant population dynamics, community structures and ecosystem functioning, mycorrhizal ecology has emerged as a fast growing subdiscipline in the field of ecology. Over recent decades, studies have expanded from descriptions of basic mycorrhizal biology to investigations of their functional relevance in a broader ecological context. Today's research is dominated by the search for underlying mechanisms and general principles. The readings on issues related to mycorrhizal ecology include basic overviews of mycorrhizal studies, classification and species diversity, methodology in mycorrhizal examination, costs and benefits, population and community ecology of mycorrhizae, their ecological significance in plant community and ecosystem, multitrophic interactions, and practical applications. This bibliography focuses on the most widespread and ecologically important types of mycorrhizae—arbuscular mycorrhizae and ectomycorrhizae.

General Overviews

John Harley was among the first pioneers attempting to synthesize disparate thoughts developed in over the first century of mycorrhizal studies (Harley 1959). During the past few decades, Harley and Smith 1983, Smith and Read 1997, and Smith and Read 2008 have been recognized as standard reference books on mycorrhizae. These books provide the most comprehensive knowledge of all major types of mycorrhizal fungi, including their identity, structure, development, function, and ecological significance. Allen 1991 integrates mycorrhizae into complex ecological concepts. Van der Heijden and Sanders 2002 includes chapters authored by notable mycorrhizal ecologists who summarize the state of knowledge in their specialized fields of mycorrhizal research. Alastair Fitter, who was president of the British Ecological Society, emphasized the important roles belowground organisms play in biodiversity and ecosystem-level processes, using arbuscular mycorrhizal fungi as a case study (Fitter 2005). Koide and Mosse 2004 is a recent review describing historical development of research on arbuscular mycorrhizae.

Allen, Michael F. 1991. *The ecology of mycorrhizae*. New York: Cambridge Univ. Press.

An excellent book that integrates mycorrhizae into complex ecological mechanisms of plant population dynamics, community structures, ecosystems processes, and practical applications.

Fitter, Alastair H. 2005. Darkness visible: Reflections on underground ecology. *Journal of Ecology* 93:231–243.

Fitter, then president of the British Ecological Society, highlights the importance of arbuscular mycorrhizal fungus, an exemplary belowground organism, in understanding biodiversity and ecosystem-level processes.

Harley, John L. 1959. *The biology of mycorrhiza*. London: Leonard Hill.

This book represents one of the first attempts to synthesize disparate thoughts developed in over 100 years of mycorrhizal studies. Its 2nd edition was published in 1969.

Harley, John L., and Sally E. Smith. 1983. *Mycorrhizal symbiosis*. New York: Academic Press.

The most authoritative and informative book on mycorrhizae published at the time when mycorrhizal association became a fascinating topic. It has been acclaimed as the bible for mycorrhiza researchers, practicing scientists, and students.

Koide, Roger T., and Barbara Mosse. 2004. A history of research on arbuscular mycorrhiza. *Mycorrhiza* 14:145–163.

This article provides a unique reflection on the historical development of arbuscular mycorrhizal research. A fascinating article to read for graduate students interested in this field.

Smith, Sally E., and David J. Read. 1997. *Mycorrhizal symbiosis*. 2d ed. San Diego, CA: Academic Press.

This edition was rewritten by Smith and Read to incorporate some of the significant advances made between 1983 and 1997.

Smith, Sally E., and David J. Read. 2008. *Mycorrhizal symbiosis*. 3d ed. San Diego, CA: Academic Press.

This latest edition keeps the same structure as previous editions, with the first three sections describing general biology of main types of mycorrhizae and the fourth focusing on their ecological functioning. Advances in molecular biology are emphasized.

van der Heijden, Marcel G. A., and Ian R. Sanders. 2002. *Mycorrhizal ecology*. Berlin: Springer.

An overview of recent advances and breakthroughs by most notable mycorrhizal ecologists. Topics include roles of mycorrhizae in plant population biology, multitrophic interactions, biological diversity, ecosystem functioning, global change, and evolution.

Journals

The majority of ecological journals publish articles on the topic of mycorrhizal ecology. New Phytologist is among the first journals regularly publishing mycorrhizal researches. Some other top-ranked journals include Ecology, Ecology Letters, Journal of Ecology, Global Change Biology, Oecologia and Plant and Soil. Mycorrhiza is the only international journal devoted to publishing research on mycorrhizae.

Ecology.

Published for the Ecological Society of America, this journal publishes articles on basic and applied ecology.

Ecology Letters.

Not affiliated with any particular professional society, *Ecology Letters* is a venue for rapid publication of concise papers on the ecology of all taxa that test clearly stated hypotheses.

Global Change Biology.

Publishes research that promotes the understanding of the interface between global change and biological systems.

Journal of Ecology.

An international journal published for the British Ecological Society since 1913, this is the oldest ecological journal and publishes research on all aspects of the ecology of plants (including algae).

Mycorrhiza.

Mycorrhiza is the official organ of the International Mycorrhiza Society. Mycorrhiza is an international journal devoted to research into mycorrhizas.

New Phytologist.

An international journal that publishes timely research in the broad principles of plant science, including physiology and development, environment, interaction, and evolution.

Oecologia.

A multidisciplinary journal publishing reviews, advances in methodology, and original studies in the areas of physiological, behavioral, population, community, ecosystem, global change, and conservation ecology.

Plant and Soil.

Published under the auspices of the Royal Netherlands Society of Agricultural Science, this journal publishes original papers and review articles exploring the interface of plant biology and soil sciences, and offering a clear mechanistic component.

Classification, Taxonomy, and Species Diversity

There are seven major types of mycorrhizae (Smith and Read 2008, cited under General Overviews), among which arbuscular mycorrhizae (AM) and ectomycorrhizae (EM) are the most widespread and prominent groups. Taxonomic classification of AM fungi has been constantly revised in recent decades. Important milestones include Gerdemann and Trappe 1974, Morton and Benny 1990, and Morton and Redecker 2001. Based on the analysis of small subunit (SSU) rRNA gene sequences, Schüssler, et al. 2001 proposed the separation of AM fungi from all other major fungal groups to form a monophyletic phylum, the Glomeromycota. AM fungal species diversity is traditionally viewed as relatively low, with only about 150 described species based on AM spore morphologies (Morton and Benny 1990), but it is generally believed that AM fungal species richness is greater than what can be morphologically described (Bever, et al. 2001). Further, DNA-based molecular approaches have revealed that extensive genetic variation exists within natural populations or within a single morphospecies (Koch, et al. 2004). EM fungi belong to several different phyla: Basidiomycota, Ascomycota, and Zygomycota. Earlier studies estimated the number of EM fungal species to be over 5,000 (Molina, et al. 1992), but a more recent survey by Rinaldi, et al. 2008 increased this number to at least 7,750 species and further predicts the actual species richness could be as high as 25,000.

Bever, James D., Peggy A. Schultz, Anne Pringle, and Joseph B. Morton. 2001. Arbuscular mycorrhizal fungi: More diverse than meets the eye, and the ecological tale of why. *Bioscience* 51:923–931.

Reported a remarkably high number of AM species within a one-hectare field, one-third of which had not been described.

Gerdemann, James W., and James M. Trappe. 1974. The Endogonaceae in the Pacific Northwest. *Mycologia Memoir* 5:1–76.

Describes three genera of AM fungi, *Glomus, Acaulospora* and *Gigaspora*, all of which are placed in the family Endogonaceae.

Koch, Alexander M., Gerrit Kuhn, Pierre Fontanillas, Luca Fumagalli, Jérôme Goudet, and Ian R. Sanders. 2004. High genetic variability and low local diversity in a population of arbuscular mycorrhizal fungi. *Proceedings of the National Academy of Sciences of the United States of America* 101:2369–2374.

Showed high genetic and phenotypic variation within *Glomus intraradices* in a small field.

Molina, Randy, Hugues Massicotte, and James M. Trappe. 1992. Specificity phenomena in mycorrhizal symbiosis: Community ecological consequences and practical application. In *Mycorrhizal functioning*. Edited by Michael F. Allen, 357–423. New York: Chapman & Hall.

Provided an estimate of EM diversity to be 5,000–6,000 species.

Morton, Joseph B., and Gerald L. Benny. 1990. Revised classification of arbuscular mycorrhizal fungi (Zygomycetes)—a new order, Glomales, 2 new suborders, Glomineae and Gigasporineae, and 2 new families, Acaulosporaceae and Gigasporaceae, with an emendation of Glomaceae. *Mycotaxon* 37:471–491.

Established a new order Glomales in the Zygomycota, comprising six genera of AM fungi.

Morton, Joseph B., and Dirk Redecker. 2001. Two new families of Glomales, Archaeosporaceae and Paraglomaceae, with two new genera *Archaeospora* and *Paraglomus*, based on concordant molecular and morphological characters. *Mycologia* 93:181–195.

This work added two more families, Archaeosporaceae and Paraglomaceae, to the order of Glomales, each consisting of one genus.

Rinaldi, Andrea C., Ornella Comandini, and Thomas W. Kuyper. 2008. Ectomycorrhizal fungal diversity: Separating the wheat from the chaff. *Fungal Diversity* 33:1–45.

Based on a thorough literature search, a conservative estimate of EM fungal species richness of 7,750 was made and the actual number of species was predicted to be as high as 25,000.

Schüssler, Arthur, Daniel Schwarzott, and Chris Walker. 2001. A new fungal phylum, the Glomeromycota: phylogeny and evolution. *Mycological Research* 105:1413–1421.

Used molecular analysis to establish the phylogenetic relationships among AM fungi and between AM fungi and other fungi. This work promotes AM fungi to form a distinct phylum, the Glomeromycota.

Classic Examination Tools

Identification of mycorrhizal fungal species and quantification of their occurrence, biomass, and functional activity are the basis for any ecological studies. Methodology has constantly evolved, but some classic tools remain on the list of essential protocols in mycorrhizal research labs. For morphological species identification, Schenck and Pérez 1990 is the most referred-to manual for AM fungi, and Agerer 1987–2002 serves as a standard guide for EM fungi. Traditional approaches to quantifying mycorrhizae target different structural components, such as AM spores extracted from soil (Gerdemann and Nicolson 1963), AM structures inside roots (McGonigle, et al. 1990), extraradical hyphae in soil (Sylvia 1992), and EM root tips (Brundrett, et al. 1996). Efforts targeting specific chemical components of mycorrhizae as a proxy to mycorrhizal biomass and activity include measurements of glomalin, a protein produced by AM fungi (Wright and Upadhyaya 1996), and fatty acids (Olsson, et al. 1995).

Agerer, Reinhard. 1987–2002. *Colour atlas of ectomycorrhizae*. Germany: Einhorn-Verlag, Schwäbisch Gmünd.

A standard manual for identification and illustration of EM fungi. Also describes habits and functional features. Information about new taxa has been continuously updated since 1987.

Brundrett, Mark, Neale Bougher, Bernie Dell, Tim Grove, and Nick Malajczuk. 1996. *Working with mycorrhizas in forestry and agriculture*. ACIAR Monograph 32. Canberra: Australian Centre for International Agricultural Research.

A comprehensive manual describing mycorrhizal methods and procedures used in the laboratory, nursery, natural field, and managed ecosystems. Especially useful for forest nursery and plantation managers, horticulturists, and agronomists.

Gerdemann, James W., and Tom H. Nicolson. 1963. Spores of mycorrhizal Endogone species extracted from soil by wet sieving and decanting. *Transactions of the British Mycological Society* 46:235–244.

Developed the widely accepted AM spore extraction technique through wet sieving and decanting.

McGonigle, Terence P., Murray H. Miller, David G. Evans, Gordon L. Fairchild, and Jacky A. Swan. 1990. A new method which gives an objective measure of colonization of roots by vesicular-arbuscular mycorrhizal fungi. *New Phytologist* 115:495–501.

This method of quantifying AM root colonization provides a more objective measure, and variations of this approach are still widely used.

Olsson, Pål Axel, Erland Bååth, Iver Jakobsen, and Bengt Söderström. 1995. The use of phospholipid and neutral lipid fatty-acids to estimate biomass of arbuscular mycorrhizal fungi in soil. *Mycological Research* 99:623–627.

The first study using phospholipid fatty acids to quantify the biomass of AM fungi in plant roots.

Schenck, Norman C., and Yvonne Pérez. 1990. *Manual for the identification of VA mycorrhizal fungi*. Gainesville, FL: Synergistic Publications.

A morphology-based species identification guide for AM fungi.

Sylvia, David M. 1992. Quantification of external hyphae of vesicular-arbuscular mycorrhizal fungi. *Methods in Microbiology* 24:53–65.

Describes techniques for quantifying AM hyphae in soil, including direct and indirect methods for measuring total hyphae, and methods for detecting active hyphae.

Wright, Sara F., and Abha Upadhyaya. 1996. Extraction of an abundant and unusual protein from soil and comparison with hyphal protein of arbuscular mycorrhizal fungi. *Soil Science* 161:575–586.

A pioneering work in the discovery of glomalin, a glycoprotein produced by AM fungi. Later work showed that glomalin plays a role in the formation of soil aggregates and contributes to their stability.

Molecular Detection

Application of molecular methods in mycorrhizal research has gained increasing popularity since the early 1990s. Bruns and his associates pioneered the use of PCR and ribosomal genes, especially ITS regions, coupled with restriction digestion to identify EM species, as seen in Gardes, et al. 1991, Gardes and Bruns 1993, and Gardes and Bruns 1996. Direct sequence analysis became a routine for more recent EM studies, such as Bruns, et al. 1998. Simon, et al. 1992 was among the first studies to introduce similar PCR-based methods to detect AM species. Later studies with revised PCR primers extended the molecular application to field experiments (Clapp, et al. 1995; Vandenkoornhuyse, et al. 2002). Molecular tools have enhanced mycorrhizal ecologists' ability to better detect mycorrhizal species, but the quantitative aspect of these methods has not been fully addressed (Horton and Bruns 2001).

Bruns, Thomas D., Timothy M. Szaro, Monique Gardes, et al. 1998. A sequence database for the identification of ectomycorrhizal basidiomycetes by phylogenetic analysis. *Molecular Ecology* 7:257–272.

A mitochondrial LSU sequence database for EM fungi was initiated in this study. The start of using direct sequence analysis to identify mycorrhizal fungal species.

Clapp, Justin P., J. Peter W. Young, James W. Merryweather, and Alastair H. Fitter. 1995. Diversity of fungal symbionts in arbuscular mycorrhizas from a natural community. *New Phytologist* 130:259–265.

One of the pioneering works using molecular methods to identify AM fungal species within roots in natural plant communities. It also revealed that molecular IDs and spore surveys do not always corroborate each other.

Gardes, Monique, and Thomas D. Bruns. 1993. ITS primers with enhanced specificity for basidiomycetes: Application to the identification of mycorrhizae and rusts. *Molecular Ecology* 2:113–118.

ITS primers reported in this study, ITS1F in particular, have been widely used for ectomycorrhizal fungal detection and identification. Molecular ecology of ectomycorrhizal fungi became popular after this.

Gardes, Monique, and Thomas D. Bruns. 1996. Community structure of ectomycorrhizal fungi in a *Pinus muricata* forest: Above- and below-ground views. *Canadian Journal of Botany-Revue Canadienne de Botanique* 74:1572–1583.

A classic study combining morphological and molecular tools to simultaneously examine both above- and belowground EM fungal community structures. It revealed a poor correspondence between aboveground sporocarp records and belowground mycorrhizal occurrences. One of the explanations for such discrepancy is that mycorrhizal species vary in their resource allocation to fruit bodies versus ectomycorrhizae.

Gardes, Monique, Thomas J. White, J. André Fortin, Thomas D. Bruns, and John W. Taylor. 1991. Identification of indigenous and introduced symbiotic fungi in ectomycorrhizae by amplification of nuclear and mitochondrial ribosomal DNA. *Canadian Journal of Botany-Revue Canadienne de Botanique* 69:180–190.

The first application of PCR-based molecular methods in mycorrhizal studies. PCR primers were developed to amplify partial regions of the internal transcribed spacer (ITS) of nuclear rDNA and the large subunit of mitochondrial rDNA.

Horton, Thomas R., and Thomas D. Bruns. 2001. The molecular revolution in ectomycorrhizal ecology: Peeking into the black-box. *Molecular Ecology* 10:1855–1871.

Reviews the progress and obstacles in the molecular ecology of mycorrhizae a few years after molecular tools became available to mycorrhizal researchers. Some suggestions, such as the use of direct sequencing for species identification, are still valid.

Simon, Luc, Maurice Lalonde, and Thomas D. Bruns. 1992. Specific amplification of 18S fungal ribosomal genes from vesicular-arbuscular endomycorrhizal fungi colonizing roots. *Applied and Environmental Microbiology* 58:291–295.

This work represents the very first attempt to develop PCR primers specifically targeting AM fungal species. Although its success was limited and the primer VANS1 reported in this study is no longer chosen by many AM researchers, this work triggered the search for AM-specific primers, which is still ongoing, and promoted the development of related molecular tools.

Vandenkoornhuyse, Philippe, Rebecca Husband, Tim J. Daniell, et al. 2002. Arbuscular mycorrhizal community composition associated with two plant species in a grassland ecosystem. *Molecular Ecology* 11:1555–1564.

Using restriction fragment length polymorphism (RFLP) profiles to characterize fungal communities, this study revealed distinct AM fungal communities associated with two coexisting grass species, providing strong evidence for AM fungal host-specificity.

Cost and Benefit

Mycorrhiza is generally viewed as a mutualistic association in which fungal partners provide nutritional benefits, enhanced water relations, protection from pathogens, and heavy metal tolerance in exchange for plant carbon (Smith and Read 2008). Facilitating the uptake of mineral nutrients, especially soil phosphorus (P) and nitrogen (N), is the most characterized mycorrhizal benefit to host plants. Smith, et al. 2003 provides evidence showing that P acquisition through mycorrhiza can be the dominant pathway of plant P uptake. Evidence has been accumulating showing that mycorrhizae can also help plants gain nutrients from organic material. For example, Leigh, et al. 2009 reports that AM fungi are able to transfer N from organic sources to host plants. Whether mycorrhizal associations are truly mutualistic is determined by the net balance of its costs and benefits (Tinker, et al. 1994). Johnson, et al. 1997 suggests that plant responses to mycorrhiza range from positive to negative depending on particular biotic and abiotic factors. Hoeksema, et al. 2010 reports a recent multi-factor meta-analysis of an extensive database and finds that plant functional group and N-fertilization are the most important factors in determining the outcome of plant responses to mycorrhiza. Understanding the costs and benefits of mycorrhiza across different plants, fungi, and environmental conditions is central for studying mycorrhizal functioning in plant community and ecosystem perspectives (Fitter 1991). Understanding how mutualism persists in the face of costs of mutualism to the fungi is also a critical question for understanding the stability of plants' benefit from this association. Bever, et al. 2009 provides evidence that the proliferation of less beneficial fungi may be prevented by the preferential allocation of carbon resources toward the most effective isolates.

Bever, James D., Sarah C. Richardson, Brandy M. Lawrence, Jonathan Holmes, and Maxine Watson. 2009. Preferential allocation to beneficial symbiont with spatial structure maintains mycorrhizal mutualism. *Ecology Letters* 12:13–21.

This study used C-14 radioactive labeling in a split-root design to provide the first evidence for preferential allocation of C by host plants to the more beneficial AM fungus. It further showed that preferential allocation can stabilize the mutualism by preventing the spread of less beneficial symbionts provided there is sufficient spatial separation between fungi.

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

This review paper first analyzed the conditions under which host plants can benefit from mycorrhizal association, and then described one of the first cost-benefit models for AM.

Hoeksema, Jason D., V. Bala Chaudhary, Catherine A. Gehring, et al. 2010. A meta-analysis of context-dependency in plant response to inoculation with mycorrhizal fungi. *Ecology Letters* 13:394–407.

Through a sophisticated multiple-factors meta-analysis of the extensive literature on plant response to inoculation, the team reports that plant functional group and N-fertilization are the most important factors in determining the outcome of plant responses to mycorrhiza.

Johnson, Nancy C., James H. Graham, and Frank A. Smith. 1997. Functioning of mycorrhizal associations along the mutualism-parasitism continuum. *New Phytologist* 135:575–586.

A touchstone synthesis paper, explicitly stating that mycorrhizal fungi can be beneficial or parasitic to host plants.

Leigh, Joanne, Angela Hodge, and Alastair H. Fitter. 2009. Arbuscular mycorrhizal fungi can transfer substantial amounts of nitrogen to their host plant from organic material. *New Phytologist* 181:199-207.

Provides direct evidence that AM fungi can capture and transfer to host plants a significant amount of N from organic material.

Smith, Sally E., and David J. Read. 2008. *Mycorrhizal symbiosis*. 3d ed. San Diego, CA: Academic Press.

The most authoritative and informative book on mycorrhiza.

Smith, Sally E., F. Andrew Smith, and Iver Jakobsen. 2003. Mycorrhizal fungi can dominate phosphate supply to plants irrespective of growth responses. *Plant Physiology* 133:16–20.

Proposed and experimentally tested two possible pathways for enhanced P uptake: direct and mycorrhizal uptake pathways. Their results showed the mycorrhizal pathway can replace direct P uptake by roots and may dominate plant P uptake even when plants do not show positive growth responses to mycorrhizal inoculation.

Tinker, Philip B., Daniel M. Durall, and Melanie D. Jones. 1994. Carbon use efficiency in mycorrhizas: Theory and sample calculations. *New Phytologist* 128:115–122.

Argued that C cost of mycorrhizal association needs to be considered when examining mycorrhizal cost-benefit relations. Developed a model of carbon use efficiency.

Population and Community Ecology

Adequate knowledge of mycorrhizal fungal population dynamics and community structure is a prerequisite for the accurate interpretation of the ecological roles mycorrhizal fungi play in ecosystems. On the one hand, there exists intrinsic variation in life history strategies among mycorrhizal fungi (Agerer 2001, Hart and Reader 2002). On the other hand, biotic and abiotic environmental factors can also influence the occurrence of particular fungal species (Abbott and Robson 1991). Johnson, et al. 1992 suggested that both plant identity and edaphic properties are of equal importance in determining community composition of AM fungi. In the search for mechanisms underlying species coexistence, Bever, et al. 1996 found that fungal population growth rates vary with host plant species, and this host-dependence could play an important role in maintaining AM fungal species diversity. More generally, niche differentiation among mycorrhizal fungi has been widely observed in field studies as a key mechanism shaping mycorrhizal population dynamics and maintaining community diversity (Taylor and Bruns 1999; Dickie, et al. 2002). Another potentially important aspect of mycorrhizal fungal community ecology is local adaptation. A recent study revealed that resource limitation is a driving force in the local adaptation of mycorrhizal symbioses (Johnson, et al. 2010).

Abbott, Lynette K., and Alan D. Robson. 1991. Factors influencing the occurrence of vesicular arbuscular mycorrhizas. *Agriculture Ecosystems and Environment* 35:121–150.

A review of the distribution and abundance of AM fungi in natural and agricultural ecosystems, and the factors influencing the occurrence of mycorrhizae, including soil properties, seasonal variation, vegetation, and disturbance.

Agerer, Reinhard. 2001. Exploration types of ectomycorrhizae: A proposal to classify ectomycorrhizal mycelial systems according to their patterns of differentiation and putative ecological importance. *Mycorrhiza* 11:107–114.

Argues that development and differentiation of the extramatrical mycelium are ecologically important features of EM fungi and can be used to classify function within this group of mycorrhizal fungi.

Bever, James D., Joseph B. Morton, Janis Antonovics, and Peggy A. Schultz. 1996. Host-dependent sporulation and species diversity of arbuscular mycorrhizal fungi in a mown grassland. *Journal of Ecology* 84:71–82.

This paper used a greenhouse mesocosm and parallel field sampling to demonstrate that sporulation and fitness of AM fungi vary with plant host species. Host-dependent fungal population growth observed here could play an important role in maintaining AM fungal species diversity.

Dickie, Ian A., Bing Xu, and Roger T. Koide. 2002. Vertical niche differentiation of ectomycorrhizal hyphae in soil as shown by T-RFLP analysis. *New Phytologist* 156:527–535.

Vertical distribution of EM fungal hyphae was tested and a pattern of spatial partitioning along the substrate-resource gradient was observed. The apparent vertical niche differentiation could be an important mechanism maintaining the diversity of mycorrhizal fungi.

Hart, Miranda M., and Richard J. Reader. 2002. Taxonomic basis for variation in the colonization strategy of arbuscular mycorrhizal fungi. *New Phytologist* 153:335–344.

Compared root colonization rate and extent of twenty-one AM fungal isolates in three families. Data showed that the colonization and growth strategies of AM fungi are different, and the difference is taxonomically based.

Johnson, Nancy C., David Tilman, and David Wedin. 1992. Plant and soil controls on mycorrhizal fungal communities. *Ecology* 73:2034–2042.

Results obtained from a classic field experiment support the hypothesis that both host plant identities and soil factors are important in controlling community composition of AM fungi.

Johnson, Nancy C., Gail W. T. Wilson, Matthew A. Bowker, Jacqueline A. Wilson, and R. Michael Miller. 2010. Resource limitation is a driver of local adaptation in mycorrhizal symbioses. *Proceedings of the National Academy of Sciences of the United States of America* 107:2093–2098.

A recent study with clear evidence showing locally adapted mycorrhizal association is more mutualistic than exotic combinations of plants, fungi, and soils.

Taylor, D. Lee., and Thomas D. Bruns. 1999. Community structure of ectomycorrhizal fungi in a *Pinus muricata* forest: Minimal overlap between the mature forest and resistant propagule communities. *Molecular Ecology* 8:1837–1850.

This study shows that EM fungal communities on mature roots and EM fungal propagules in soil in a *Pinus muricata* forest shared very little in terms of species abundance, frequency, and spatial distribution. The results indicate that EM species differences in colonization strategies and resource utilization play a role in maintaining species diversity in a natural fungal community.

Mycorrhizae and Plant Community Dynamics

The ecological impact of mycorrhizal fungi on plant communities has been a central theme in studies of mycorrhizal ecology. A large body of work has addressed various roles mycorrhizae play in shaping plant community structure (van der Heijden, et al. 1998; Hartnett and Wilson 1999), facilitating plant succession (Nara and Hogetsu 2004), and promoting native plant adaptation (Klironomos 2003). Efforts to integrate mycorrhizal components into broader theories of plant community dynamics continue. Bever, et al. 2010 articulates three mechanisms through which soil microbial processes, including mycorrhizal symbiosis, could mediate plant-plant interactions and thereby structure plant communities. One mechanism is resource partitioning as a result of functional variation in mycorrhizal fungi, which was emphasized by Newsham, et al. 1995 and numerous other studies. Another is resource sharing facilitated by a common mycorrhizal network, a topic that gained attention following the classic labeling studies of Simard, et al. 1997. The third mechanism is plant-soil feedback as a consequence of host-specificity of mycorrhizal fungi, as demonstrated by Bever 2002.

Bever, James D. 2002. Negative feedback within a mutualism: Host-specific growth of mycorrhizal fungi reduces plant benefit. *Proceedings of the Royal Society of London Series B-Biological Sciences* 269:2595–2601.

This mesocosm study demonstrated that AM fungal community composition shifted with plant host, and an individual plant species grew more poorly with their own differentiated fungal community than with that of its competing plant species. This mycorrhiza-mediated negative feedback may serve as an underlying mechanism for plant species coexistence.

Bever, James D., Ian A. Dickie, Evelina Facelli, et al. 2010. Rooting theories of plant community ecology in microbial interactions. *Trends in Ecology and Evolution* 25:468–478.

A perspective paper that integrates soil microbial components into current theories of plant community dynamics. Three mechanisms —microbial-mediated niche modification, plant–soil community feedbacks, and common mycorrhizal networks—are discussed.

Hartnett, David C., and Gail W. T. Wilson. 1999. Mycorrhizae influence plant community structure and diversity in tallgrass prairie. *Ecology* 80:1187–1195.

Another classic study demonstrating that AM fungi play important roles in structuring plant communities in the field when host plants vary in their responses to fungal colonization.

Klironomos, John N. 2003. Variation in plant response to native and exotic arbuscular mycorrhizal fungi. *Ecology* 84:2292–2301.

This influential article demonstrates that plant response to mycorrhizae depends on the combination of plant and fungal species. Native combinations of plants and fungi beget the greatest variation in plant responses, whereas exotic combinations result in less variable responses.

Nara, Kazuhide, and Taizo Hogetsu. 2004. Ectomycorrhizal fungi on established shrubs facilitate subsequent seedling establishment of successional plant species. *Ecology* 85:1700–1707.

Through the comparisons of EM fungal communities on a pioneer plant species and three successional plant species in an early successional field, this study reveals the importance of EM fungi in facilitating vegetation recovery and plant succession during early primary succession.

Newsham, Kevin K., Alastair H. Fitter, and Andrew R. Watkinson. 1995. Multi-functionality and biodiversity in arbuscular mycorrhizas. *Trends in Ecology and Evolution* 10:407–411.

A strong message delivered by this review is that the ecological functionality of mycorrhizal fungi beyond the facilitation of P uptake needs to be considered. Other types of benefits, especially protection from soil pathogens, may be equally important in natural communities.

Simard, Suzanne W., David A. Perry, Melanie D. Jones, David D. Myrold, Daniel M. Durall, and Randy Molina. 1997. Net transfer of carbon between ectomycorrhizal tree species in the field. *Nature* 388:579–582.

This paper presents evidence of carbon transfer through ectomycorrhizal hyphae. This work motivated a large body of work on potential ecological significance of mycorrhizal mediation of carbon transfer between plant species.

van der Heijden, Marcel G. A., Thomas Boller, Andres Wiemken, and Ian R. Sanders. 1998. Different arbuscular mycorrhizal fungal species are potential determinants of plant community structure. *Ecology* 79:2082–2091.

A greenhouse inoculation study showing that plant species differ in their mycorrhizal dependency, and AM fungal species (both individual species and species in combination) vary in promoting growth of different plant species.

Mycorrhizae and Ecosystem Functioning

Since around 1990, mycorrhizal ecologists have extended the knowledge of the structure and function of mycorrhizal symbiosis in individual roots, single plants, and isolated communities to the ecosystem level. Great advances have been made in understanding the global distribution of mycorrhizae and the roles mycorrhizal fungi play in key ecosystem processes, nutrient cycling, and soil stability. In a review to summarize the functional roles of major types of mycorrhizae within their characteristic ecosystems, Read 1991 claimed that the spatial segregation of major mycorrhizal types and their respective biomes is a result of nutritional niche differentiation. Evidence obtained from various ecosystems, with different types of mycorrhizae, and using a variety of approaches generally supported the idea that mycorrhizae play critical roles in ecosystem biodiversity and productivity (van der Heijden, et al. 1998; Vogelsang, et al. 2006), C cycling (Jakobsen and Rosendahl 1990, Rygiewicz and Andersen 1994), N and P cycling (Hobbie, et al. 1999; Blum, et al. 2002), and soil stability (Rillig and Mummey 2006).

Blum, Joel D., Andrea Klaue, Carmen A. Nezat, et al. 2002. Mycorrhizal weathering of apatite as an important calcium source in base-poor forest ecosystems. *Nature* 417:729–731.

Data suggest that EM fungi might help weather calcium phosphate and provide host plants with bio-available calcium in a base-poor forest.

Hobbie, Erik A., Stephen A. Macko, and Herman H. Shugart. 1999. Insights into nitrogen and carbon dynamics of ectomycorrhizal and saprotrophic fungi from isotopic evidence. *Oecologia* 118:353–360.

A pioneering study using stable isotope analysis to study the roles of mycorrhizal fungi in ecosystem N and C cycling. Its results showed that plant N supply through mycorrhizal fungi increases when N in soil is more limiting.

Jakobsen, Iver, and Lis Rosendahl. 1990. Carbon flow into soil and external hyphae from roots of mycorrhizal cucumber

plants. *New Phytologist* 115:77–83.

Through C-14 labeling of a cucumber plant and subsequent measurements of C-14 flow into soil and AM fungus, this work estimated that about 20 percent of plant-fixed C was allocated to mycorrhiza, the highest percentage reported so far.

Read, David J. 1991. Mycorrhizas in ecosystems. *Experientia* 47:376–391.

Summarizes the roles of major types of mycorrhizae within their characteristic ecosystems: AM in grassland, EM in forest, and Ericoid in heathland. The central role of mycorrhizae is to provide host plants with key limiting nutrients. On a global scale, the spatial segregation of major mycorrhizal types and their respective biomes is likely to be a result of nutritional niche differentiation among distinct mycorrhizal associations.

Rillig, Matthias C., and Daniel L. Mummey. 2006. Mycorrhizas and soil structure. *New Phytologist* 171:41–53.

This paper reviews the contribution of mycorrhiza to soil structure. The influence of mycorrhizal fungi on the formation of soil aggregates is discussed at three different scales: plant community, individual root, and soil mycelium. The authors argue that promoting soil aggregation should be considered as an important function of mycorrhiza.

Rygiewicz, Paul T., and Christian P. Andersen. 1994. Mycorrhizae alter quality and quantity of carbon allocated below ground. *Nature* 369:58–60.

A study that directly measured C fluxes through all major pools of EM inoculated ponderosa pine seedlings. The complete carbon budget constructed in this study showed that about 4.3 percent of plant-fixed C was allocated to fungus. However, more than half of the C received was respired by fungus. They concluded that mycorrhiza reduces overall carbon retention in the plant-fungus symbiosis by increasing carbon in roots and belowground respiration.

van der Heijden, Marcel G. A., John N. Klironomos, Margot Ursic, et al. 1998. Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. *Nature* 396:69–72.

This study provided the first evidence that AM fungal community composition and species richness are determinants of plant community composition, ecosystem variability, and productivity.

Vogelsang, Keith M., Heather L. Reynolds, and James D. Bever. 2006. Mycorrhizal fungal identity and richness determine the diversity and productivity of a tallgrass prairie system. *New Phytologist* 172:554–562.

This study finds that the identity of AM fungi has a large effect on plant community diversity and productivity, and that increased likelihood of including the most effective fungi can generate the positive effect of AM fungal species richness on plant community diversity and productivity.

Multi-Trophic Interactions

Plant and mycorrhizal fungi interact with a wide range of other organisms, including soil bacteria, herbivores, soil invertebrates, and saprotrophic fungi. Some of these multi-trophic interactions have positive impacts on mycorrhizal mutualism. For example, mycorrhizal fungi can directly suppress the growth of root pathogenic fungi and bacteria, thus offering protective benefits to host plants (Marx 1969). Certain soil organisms are beneficial to mycorrhizal fungi by directly promoting the establishment and development of mycorrhizal association (Garbaye 1994) or by preferentially feeding on non-mycorrhizal microbes (Gange 2000). Some other multi-trophic interactions have inhibiting impacts on mycorrhiza. For example, aboveground herbivores often negatively affect mycorrhizal colonization by reducing plant carbon allocation to belowground mutualists (Gehring and Whitham 1991). As reviewed by Fitter and

Garbaye 1994, multi-trophic interactions in mycorrhizal plants are complex. The outcomes can be either inhibitory or stimulatory, and the mutual effects are either symmetrical or asymmetrical. The direction and intensity of these interactions depend on many factors, including the identities of interacting organisms and their life history strategies (Koricheva, et al. 2009), as well as the species identity of the mycorrhizal fungi (Bennett and Bever 2007).

Bennett, Alison E., and James D. Bever. 2007. Mycorrhizal species differentially alter plant growth and response to herbivory. *Ecology* 88:210–218.

An important finding from this study is that the direction and magnitude of plant response to herbivory change depending on the particular fungal species with which the plant forms mycorrhizae.

Fitter, Alastair H., and Jean Garbaye. 1994. Interactions between mycorrhizal fungi and other soil organisms. *Plant and Soil* 159:123–132.

A review of mycorrhizal interactions with various types of soil microbes, the nature and effects of these interactions, and the importance of studying them in natural ecosystems.

Gange, Alan. 2000. Arbuscular mycorrhizal fungi, *Collembola* and plant growth. *Trends in Ecology and Evolution* 15:369–372.

Review paper in which the author argues that mycophagous animals such as *Collembola* may preferentially feed on non-mycorrhizal fungi in the rhizosphere, thus benefiting mycorrhizal functioning and positively affecting plant growth.

Garbaye, Jean 1994. Helper bacteria: A new dimension to the mycorrhizal symbiosis. *New Phytologist* 128:197–210.

A review of bacteria that promote mycorrhizal establishment, development, and functioning. Some fundamental aspects of these mycorrhizal helper bacteria are discussed, including their fungal specificity, mechanisms underlying their effect, their ecological and evolutionary implications, and practical applications.

Gehring, Catherine A., and Thomas G. Whitham. 1991. Herbivore-driven mycorrhizal mutualism in insect-susceptible pinyon pine. *Nature* 353:556–557.

Levels of ectomycorrhizal colonization were examined between pinyon pines that are resistant or susceptible to an insect herbivore. Results show that aboveground herbivores suppress belowground mycorrhizal association. Removal of insect herbivores from susceptible trees increases mycorrhizal colonization to a level that is comparable to that of resistant trees.

Koricheva, Julia, Alan C. Gange, and Tara Jones. 2009. Effects of mycorrhizal fungi on insect herbivores: A meta-analysis. *Ecology* 90:2088–2097.

This recent meta-analysis paper finds that the sources of variation in mycorrhizal effects on insect herbivores depend on the feeding mode and diet breadth of the insects, and the identity of the fungi.

Marx, Donald H. 1969. Influence of ectotrophic mycorrhizal fungi on resistance of pine roots to pathogenic infections: I. Antagonism of mycorrhizal fungi to root pathogenic fungi and soil bacteria. *Phytopathology* 59:153–163.

One of the first studies that provided direct evidence showing that EM fungi can inhibit the growth of a variety of root pathogenic fungi and bacteria. The study was conducted in the laboratory with agar plate culturing.

Wamberg, Camilla, Søren Christensen, Iver Jakobsen, Anne K. Muller, and Søren J. Sørensen. 2003. The mycorrhizal fungus (*Glomus intraradices*) affects microbial activity in the rhizosphere of pea plants (*Pisum sativum*). *Soil Biology and Biochemistry* 35:1349–1357.

This study reports that AM fungi influence microbial community composition (protozoa and bacteria) and microbial activity (respiration) in the rhizosphere of a pea plant, and the influence varies with different growth phases of the plant.

Mycorrhizae and Global Change

Studies of mycorrhizae in relation to global change face unique challenges because a multitude of factors and their complex interactions, larger-scale processes, and longer-term responses need to be considered. However, progress has been made regarding a few key climate change factors, including warming, elevated CO^2, nitrogen deposition, and altered precipitation (Rillig, et al. 2002). The C budget is a major research topic within global change. When the effect of increased soil temperature is examined in a mycorrhizal system, more C is predicted to be released from the soil into the atmosphere owing to increased AM fungal respiration (Hawkes, et al. 2008). However, Treseder and Allen 2000 suggests that mycorrhizal fungi can be either a net sink or a net source of C under the conditions of elevated CO^2 and increased N input. Mycorrhizae can also mediate the effects of global change on plants, but this mediation is shown to be fungal species-specific (Gorissen and Kuyper 2000). More studies have looked at how global change would affect mycorrhizae. Staddon, et al. 2003 demonstrated that summer drought increases AM root colonization and extraradical hyphal production, but elevated CO^2 does not (Staddon, et al. 1999). N deposition is shown to change mycorrhizal community composition (Egerton-Warburton, et al. 2000; Lilleskov, et al. 2002).

Egerton-Warburton, Louise M., and Edith B. Allen. 2000. Shifts in arbuscular mycorrhizal communities along an anthropogenic nitrogen deposition gradient. *Ecological Applications* 10:484–496.

This study conducted both N fertilization experiments and direct field survey along an anthropogenic nitrogen deposition gradient to investigate how an AM fungal community responds to N deposition. A few patterns were observed with the increases in N input: AM fungal community composition shift from larger-spored species to small-spored species; decrease in AM species richness and diversity; and reduced spore production, hyphal density, and root colonization rate.

Gorissen, Antonie, and Thomas W. Kuyper. 2000. Fungal species-specific responses of ectomycorrhizal Scots pine (*Pinus sylvestris*) to elevated CO_2. *New Phytologist* 146:163–168.

Results demonstrate that Scots pine seedlings respond to elevated CO^2 differently when inoculated with two different EM fungal species, suggesting that plant response to global change can be fungal species-specific.

Hawkes, Christine V., Iain P. Hartley, Phil Ineson, and Alastair H. Fitter. 2008. Soil temperature affects carbon allocation within arbuscular mycorrhizal networks and carbon transport from plant to fungus. *Global Change Biology* 14:1181–1190.

This research paper reports how mycorrhizae respond to different soil temperatures in terms of C allocation within mycorrhizal components and C flux from plant to fungus. Warming enhances extraradical hyphal growth, increases C flow from plant to belowground, and boosts the respiration of roots and fungi. The authors predict that under global warming more carbon would be released to the atmosphere as a result of increased AM fungal respiration.

Lilleskov, Erik A., Timothy J. Fahey, Thomas R. Horton, and Gary M. Lovett. 2002. Belowground ectomycorrhizal fungal community change over a nitrogen deposition gradient in Alaska. *Ecology* 83:104–115.

This study looked at EM fungal community change along an N deposition gradient. Patterns similar to those found in AM studies were observed: dramatic decline in EM fungal species richness and complete change in dominant fungal species with the increase in N deposition.

Rillig, Matthias, Kathleen K. Treseder, and Michael F. Allen. 2002. Global change and mycorrhizal fungi. In *Mycorrhizal ecology*. Edited by Marcel van der Heijden and Ian R. Sanders, 135–160. Berlin: Springer.

A book chapter in which the authors discuss mycorrhizal responses to various global change factors, including elevated CO2, N deposition, altered temperature and precipitation, and others. The authors emphasize the need for studies on multifactor interactions and long-term effects.

Staddon, Philip L., Alastair H. Fitter, and Jonathan D. Graves. 1999. Effect of elevated atmospheric CO_2 on mycorrhizal colonization, external mycorrhizal hyphal production and phosphorus inflow in *Plantago lanceolata* and *Trifolium repens* in association with the arbuscular mycorrhizal fungus *Glomus mosseae*. *Global Change Biology* 5:347–358.

Authors of this study argue that when analyzing mycorrhizal response to elevated CO^2, changes in plant developmental stage should be taken into account as a covariate. Their results reveal that elevated CO^2 has little direct effect on mycorrhizal root colonization or external hyphal production, a pattern contrary to what many previous studies have reported.

Staddon, Philip L., Ken Thompson, Iver Jakobsen, J. Philip Grime, Andrew P. Askew, and Alastair H. Fitter. 2003. Mycorrhizal fungal abundance is affected by long-term climatic manipulations in the field. *Global Change Biology* 9:186–194.

A field study that examines AM fungal responses to long-term (after seven-year treatments), multifactor climatic manipulations. Summer drought has the strongest effect on AM root colonization levels and extraradical mycorrhizal hyphal density.

Treseder, Kathleen K., and Michael F. Allen. 2000. The potential role of mycorrhizal fungi in soil carbon storage under elevated CO_2 and nitrogen deposition. *New Phytologist* 147:189–200.

A review discussing the scenarios in which mycorrhizal fungi may act as either net sink or net source of C under conditions of elevated CO^2 and N deposition. The authors suggest that analyzing mycorrhizal fungal turnover and community composition shift would improve understanding of mycorrhizal C dynamics.

Applications in Managed Ecosystems

Ecological studies of mycorrhizal fungi have provided theoretical bases and practical guidelines for applying mycorrhizae in agriculture, horticulture, and forestry. It has been long recognized that conventional agriculture has a negative impact on mycorrhizae, for instance by reducing the diversity of mycorrhizal fungi (Helgason, et al. 1998). Johnson 1993 found that long-term N fertilization could select less mutualistic fungi in soil. Similarly, clear-cutting forests can have strong negative effects on ectomycorrhizal fungal communities (Jones, et al. 2003). Besides shifts in composition, the presence of mycorrhizal fungi could have no or even negative impact on plant growth under certain conditions, such as in P-rich soil (Peng, et al. 1993; Li, et al. 2006). These findings have far-reaching implications for effective management of mycorrhizae in practice. Appropriate uses of mycorrhizae could help soil fertility and plant health (Jeffries, et al. 2003). There are many successful cases of applying mycorrhiza in managed ecosystems. A highly beneficial EM species, *Pisolithus tinctorius*, has been an important inoculum in loblolly pine nurseries (Marx and Bryan 1975). Before mycorrhizae can be practically used in a wider range of managed ecosystems, however, professional guidelines are needed. One such manual has been developed by Brundrett, et al. 1996 as a product of a workshop sponsored by the Australian Centre for International Agricultural Research to promote the use of mycorrhizal fungi for eucalypt plantation forestry in China.

Brundrett, Mark, Neale Bougher, Bernie Dell, Tim Grove, and Nick Malajczuk. 1996. *Working with mycorrhizas in forestry and*

***agriculture*. ACIAR Monograph 32. Canberra: Australian Centre for International Agricultural Research.**

This manual describes common procedures used by mycorrhizal researchers to work with mycorrhizal fungi in the lab, nursery or natural and managed ecosystems. Its second version, updated in 2008, is available online.

Helgason, Thorunn, Tim J. Daniell, Rebecca Husband, Alastair H. Fitter, and J. Peter W. Young. 1998. Ploughing up the wood-wide web? *Nature* 394:431.

This brief communication used environmental sampling of rRNA gene sequence variation to demonstrate a reduction in diversity of AM fungi with conventional agriculture.

Jeffries, Peter, Silvio Gianinazzi, Silvia Perotto, Katarzyna Turnau, and José-Miguel Barea. 2003. The contribution of arbuscular mycorrhizal fungi in sustainable maintenance of plant health and soil fertility. *Biology and Fertility of Soils* 37:1–16.

This paper reviews various mechanisms by which AM fungi provide key benefits to plants and play important roles in sustainable maintenance of plant health and soil fertility. Examples of AM applications in practical management discussed by the authors include landscape development, horticulture and agriculture, alleviation of desertification, and bioremediation of soils containing pollutants.

Johnson, Nancy C. 1993. Can fertilization of soil select less mutualistic mycorrhizae? *Ecological Applications* 3:749–757.

Surveys of long-term fertilization plots and greenhouse pot manipulations show that less beneficial AM assemblages are selected by chemical fertilizers. This finding has important implications for agricultural practices.

Jones, Melanie D., Daniel M. Durall, and John W. G. Cairney. 2003. Ectomycorrhizal fungal communities in young forest stands regenerating after clearcut logging. *New Phytologist* 157:399–422.

A thorough and in-depth review on how clearcut logging influences the interactions between ECM fungi and seedlings. The most important conclusion is that biological, chemical, and physical changes following clearcut logging are important drivers of EM fungal community change.

Li, Huiying, Sally E. Smith, Robert E. Holloway, Yongguan Zhu, and F. Andrew Smith. 2006. Arbuscular mycorrhizal fungi contribute to phosphorus uptake by wheat grown in a phosphorus-fixing soil even in the absence of positive growth responses. *New Phytologist* 172:536–543.

This study is an example of major crop plant showing no positive growth response to AM fungi, while gaining a significant amount P through mycorrhizal uptake.

Marx, Donald H., and William C. Bryan. 1975. Growth and ectomycorrhizal development of loblolly pine seedlings in fumigated soil infested with fungal symbiont *Pisolithus tinctorius*. *Forest Science* 21:245–254.

A practical study testing inoculation of vegetative mycelium and basidiospores of a highly beneficial EM fungus, *Pisolithus tinctorius*, in loblolly pine nurseries.

Peng, Shaobing, David M. Eissenstat, James H. Graham, Kimberlyn Williams, and Nancy C. Hodge. 1993. Growth depression in mycorrhizal citrus at high-phosphorus supply: Analysis of carbon costs. *Plant Physiology* 101:1063–1071.

After comparing respiration rates of various root-mycorrhiza components between mycorrhizal and nonmycorrhizal plants, the authors attributed the growth depression of AM-colonized citrus plant in a P-rich soil to higher C costs by mycorrhizal roots relative to nonmycorrhizal roots.

Plant Invasion and Ecological Restoration

Mycorrhiza-mediated belowground interactions can play critical roles in the inhibition or acceleration of invasion of exotic plants, and in facilitating the restoration of native vegetation. A recent review, Pringle, et al. 2009, provides a comprehensive framework in which the trajectory of plant invasion is related to key biological and ecological features of mycorrhizae. Schwartz, et al. 2006 expresses concerns about introducing foreign mycorrhizal fungi into local habitats, a topic relevant to plant invasion and restoration. Among various mechanisms through which mycorrhizae can prevent plant invasion, a particularly interesting one is that indigenous mycorrhizal fungi form beneficial associations only with native plants, not with invading species, so that native plants gain a competitive advantage (Nunez, et al. 2009). The reverse scenario would result in the opposite outcome, as observed by Stinson, et al. 2006. Mechanisms underlying mycorrhizal facilitation of ecological restoration include indigenous symbionts assisting pioneer plants to establish (Requena, et al. 2001), arbuscular mycorrhizal fungi supporting the establishment of later successional plant species (Koske and Gemma 1997), and mycelium as a binding agent of soil aggregates to improve soil stability (Jastrow, et al. 1998). In addition, the ability of mycorrhizal fungi to tolerate, take up, and accumulate heavy metals helps the restoration of polluted soil (Leyval, et al. 1997).

Jastrow, Julie D., R. Michael Miller, and John Lussenhop. 1998. Contributions of interacting biological mechanisms to soil aggregate stabilization in restored prairie. *Soil Biology and Biochemistry* 30:905–916.

This work highlights the importance of mycorrhizal hyphae in the formation and stabilization of soil aggregates, an essential component of tallgrass prairie restoration.

Koske, Richard E., and Jane Natale Gemma. 1997. Mycorrhizae and succession in plantings of beachgrass in sand dunes. *American Journal of Botany* 84:118–130.

In this study, AM fungal communities, root mycorrhizal colonization, hyphal networks, and mycorrhizal inoculum potential were examined in sand dune sites. Results revealed successional changes in mycorrhizae, indicating that restoration of the belowground symbionts is an intrinsic component of restoration of the aboveground plant community.

Leyval, Corinne, Katarzyna Turnau, and Kurt Haselwandter. 1997. Effect of heavy metal pollution on mycorrhizal colonization and function: Physiological, ecological and applied aspects. *Mycorrhiza* 7:139–153.

The authors review biological and ecological interactions between heavy metals and mycorrhizal fungi, possible mechanisms involved in metal tolerance, uptake, and accumulation by mycorrhizae, and practical uses of mycorrhizal fungi as bioremediation agents or bioindicators of polluted soils.

Nunez, Martin A., Thomas R. Horton, and Daniel Simberloff. 2009. Lack of belowground mutualisms hinders Pinaceae invasions. *Ecology* 90:2352–2359.

Greenhouse and field experimental results in this study show that the establishment and growth of invading Pinaceae tree species were suppressed by their lack of EM fungal symbionts.

Pringle, Anne, James D. Bever, Monique Gardes, Jeri L. Parrent, Matthias C. Rillig, and John N. Klironomos. 2009. Mycorrhizal symbioses and plant invasions. *Annual Review of Ecology Evolution and Systematics* 40:699–715.

A recent review relates most critical features of mycorrhizal symbiosis to the trajectory of a plant invasion.

Requena, Natalia, Estefania Perez-Solis, Concepción Azcon-Aguilar, Peter Jeffries, and José-Miguel Barea. 2001. Management of indigenous plant-microbe symbioses aids restoration of desertified ecosystems. *Applied and Environmental Microbiology* 67:495–498.

Reports a successful restoration practice in a desertified Mediterranean ecosystem through the inoculation of seedlings with native AM fungi and with indigenous rhizobial nitrogen-fixing bacteria. Indigenous symbionts helped plants to establish, and improved soil nutritional conditions.

Schwartz, Mark W., Jason D. Hoeksema, Catherine A. Gehring, et al. 2006. The promise and the potential consequences of the global transport of mycorrhizal fungal inoculum. *Ecology Letters* 9:501–515.

The authors review some key aspects of our understanding of mycorrhizal ecology and some general patterns of invasive species, and address their concerns about the unintended negative and potentially costly consequences associated with the production and application of mycorrhizal inocula. Recommendations regarding appropriate management guidelines are made from the perspective of mycorrhizal ecology.

Stinson, Kristina A., Stuart A. Campbell, Jeff R. Powell, et al. 2006. Invasive plant suppresses the growth of native tree seedlings by disrupting belowground mutualisms. *PLoS Biology* 4:727–731.

A novel mechanism is revealed in this study by which an invasive plant can eliminate the activity of native mycorrhizal fungi and therefore suppress the growth of native tree seedlings that are highly dependent on mycorrhiza.

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