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Patterns and regulation of mycorrhizal plant and fungal diversity

Edith B. Allen[1], Michael F. Allen[2], Dot J. Helm[3], James M. Trappe[4], Randy Molina[5] and Emmanuel Rincon[6]

[1]*Department of Botany and Plant Sciences, University of California, Riverside, CA 92521-0124, USA,* [2]*Department of Biology, San Diego State University, San Diego, California 92182-0057, USA,* [3]*Agriculture and Forestry Research Station, University of Alaska, Palmer, AK 99645, USA,* [4]*Department of Forest Science, Oregon State University Corvallis, OR 97331, USA,* [5]*USDA Forest Service, Forestry Sciences Laboratory, 3200 Jefferson Way, Corvallis, OR 97331, USA and* [6]*Center for Ecology, Apartado Postal 71-275, National Autonomous University of Mexico, Mexico City, Mexico*

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Abstract

The diversity of mycorrhizal fungi does not follow patterns of plant diversity, and the type of mycorrhiza may regulate plant species diversity. For instance, coniferous forests of northern latitudes may have more than 1000 species of ectomycorrhizal (EM) fungi where only a few ectomycorrhizal plant species dominate, but there are fewer than 25 species of arbuscular mycorrhizal (AM) fungi in tropical deciduous forest in Mexico with 1000 plant species. AM and EM fungi are distributed according to biome, with AM fungi predominant in arid and semiarid biomes, and EM fungi predominant in mesic biomes. In addition, AM fungi tend to be more abundant in soils of low organic matter, perhaps explaining their predominance in moist tropical forest, and EM fungi generally occur in soils with higher surface organic matter.

EM fungi are relatively selective of host plant species, while AM tend to be generalists. Similar morphotypes of AM fungi collected from different sites confer different physiological benefits to the same plant species. While the EM fungi have taxonomic diversity, the AM fungi must have physiological diversity for individual species to be so widespread, as supported by existing studies. The environmental adaptations of mycorrhizal fungi are often thought to be determined by their host plant, but we suggest that the physiology and genetics of the fungi themselves, along with their responses to the plant and the environment, regulates their diversity. We observed that one AM plant species, *Artemisia tridentata*, was associated with different fungal species across its range, indicating that the fungi can respond to the environment directly and must not do so indirectly via the host. Different species of fungi were also active during different times of the growing season on the same host, again suggesting a direct response to the environment.

These patterns suggest that even within a single "functional group" of microorganisms, mycorrhizal fungi, considerable diversity exists. A number of researchers have expressed the concept of functional redundancy within functional groups of microorganisms, implying that the loss of a few species would not be detectable in ecosystem functioning. However, there may be high functional diversity of AM fungi within and across habitats, and high species diversity as well for EM fungi. If one species of mycorrhizal fungus becomes extinct in a habitat, field experimental data on AM fungi suggest there may be significant shifts in how plants acquire resources and grow in that habitat.

Introduction

Worldwide patterns and regulation of plant species richness have long been of interest (Pianka, 1966; Rosenzweig, 1992), but less is known about the richness of the mycorrhizal fungi with which plants are associated. Plant species richness generally increases along a gradient from the poles to the tropics, but mycorrhizal fungi have exceptions to this pattern because fungal species richness varies between sites regardless

of latitude, and among types of mycorrhizal fungi that dominate any site (Malloch et al., 1980; Connell and Lowman, 1989). Because most plants are associated with mycorrhizal fungi of various types, an examination of the diversity patterns of the fungi may shed light on patterns and causes of plant species diversity. Plant species are quite well known from northern latitudes, but new species are still being discovered in the tropics. Fungal species richness is poorly studied compared to plants. Hawksworth (1991) estimated that only 5% of fungal species have been described, an estimate that was obtained by multiplying up from the known species of fungi and based on the high diversity of plants in the tropics. It likely does not take into account the ecology of the fungi, as we shall show here from existing data on worldwide diversity patterns of mycorrhizal fungi. Some especially important ecological considerations that we will discuss are that mycorrhizal fungal diversity need not necessarily be related to plant species diversity, nor correlated with latitudinal gradients. Our objectives are to present the known patterns of diversity of mycorrhizal fungi and to examine evidence for the mutual regulation of mycorrhizal plant and fungal diversity. In this paper the term richness will be defined in the usual sense as species count per unit area, and diversity will be defined as Shannon-Wiener diversity that combines richness and evenness.

Seven types of mycorrhizal fungi are currently recognized, the ectomycorrhizae, arbuscular, ericoid, arbutoid, monotropoid, orchid, and E-strain mycorrhizae (Harley and Smith, 1983). The term arbuscular mycorrhiza, rather than the more usual vesicular-arbuscular mycorrhiza is adopted here because two genera, *Scutellospora* and *Gigaspora*, do not form vesicles (Morton, 1990). The existence of seven types further complicates examination of richness of mycorrhizal fungi, and their relationships to plant species richness. These types have been studied to varying degrees, with arbuscular and ectomycorrhizal fungi receiving the most attention (Molina et al., 1992; Schenck and Perez, 1990). Others, such as the ericoid fungi, are largely unknown and unidentified (Egger and Sigler, 1993). The different types of mycorrhizal fungi have rather specific associations with different biomes and different amounts of species richness, as will be explained in more detail below for instance, plant species-poor coniferous forests may have hundreds of ectomycorrhizal (EM) fungal species (Trappe, 1977), while plant species-rich tropical forest may have only a dozen or two arbuscular mycorrhizal (AM) fungal species (Wilson et al., 1992; Allen, Allen and Rincon, unpubl. observations). Because EM and AM fungi are the most widespread and best studied, we will focus on these two types.

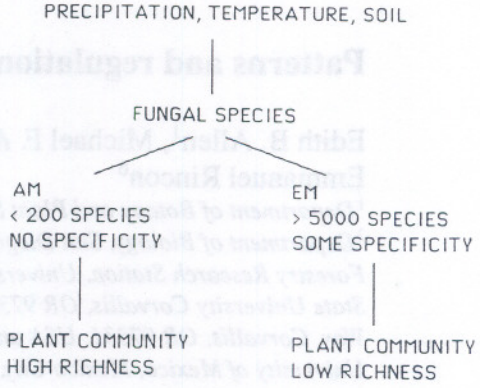

Fig. 1. Model of the relationships between environmental conditions, types of mycorrhizal fungi, and plant and fungal richness. AM = arbuscular mycorrhizal, EM = ectomycorrhizal.

The observation that the richness of mycorrhizal fungi does not follow patterns of plant species richness has been made previously (Malloch et al., 1980; Meyer, 1973; Moser, 1967), and has been much discussed by mycorrhizal researchers in informal settings. In general, AM plant communities tend to be high in plant but low in fungal species richness, while EM communities are low in plant but high in fungal richness (Fig. 1). To explain these patterns and the potential for mutual regulation between plant and fungal richness, we will address several points. The type of mycorrhizal fungus, AM or EM, may regulate the richness of the plant community, a hypothesis that has been proposed for tropical vegetation (Connell and Lowman, 1989) and may be extended to all biomes. Another major point is that, while a latitudinal gradient exists for plant richness, it does not necessarily occur for fungal richness, even within AM or EM communities. While the regulation of fungal richness along latitudinal gradients is problematic, we will discuss genetic and reproductive differences among AM and EM fungi that may explain their relative differences in richness. There have been many advances in mycorrhizal research since the mycorrhizal/plant richness concept was last published (Malloch et al., 1980; Moser, 1967), and we express views on regulation of diversity to understand these relationships. The advances include increases in the number of described species of mycorrhizal fungi, AM fungi in particular, from 31 in 1974 to 147 in 1990 (Gerdemann and Trappe, 1974; Schenck

and Perez, 1990), numerous additional surveys of AM and EM fungi in various locations worldwide that can help fill in some of the gaps of latitudinal richness patterns, and our knowledge of specificity of the EM fungi (Molina et al., 1992). In addition to these points, we conclude with a discussion on the functional diversity of mycorrhizal fungi with implications for conservation and ecosystem functioning.

Relationships between AM and EM fungi and plant species richness

To understand the diversity relationships between plants and mycorrhizal fungi, we present four observations on the ecology and natural history of AM and EM fungi that are important in how they may affect plant communities. We must first think of fungi as individual organisms with their own relationships to climate and soils (Fig. 1). Ecologists have documented that plant and animal distributions fall along gradients (Whittaker, 1975), but such distributions are poorly studied for mycorrhizal fungi. Even though mycorrhizal fungi are obligately associated with a host plant, they also have specific environmental requirements that transcend their need for a specific plant host (Koske, 1987). For instance, many species of AM fungi occur worldwide in similar types of climates (e.g. Schenck and Perez, 1990; Walker, 1992), where they associate with the resident plant species. This indicates that their distributions are influenced more by environment than by specific host-plant association. In addition, individual species of AM fungi are broad in their environmental requirements. Species such as *Glomus mosseae* or *G. fasciculatum* occur in moist forests as well as semiarid grasslands. Alternatively, these may be species complexes that are similar in morphology but dissimilar in physiology (Walker, 1992). Other species and genera are more restricted. For instance, the genera *Scutellospora* and *Acaulospora* are more diverse in the tropics than other genera, the genus *Gigaspora* has not been reported from northern Europe (Walker, 1992), and the species *Glomus australis* has been found only in Australia (Trappe, pers. obs.; Schenck and Perez, 1990). In large part, though, mycorrhiza researchers on different continents are able to use the single key by Schenck and Perez (1990) to identify their AM species, although many remain undescribed.

The EM fungi also have specific environmental requirements, although the worldwide distribution of any one species is not as great as for many AM fungi. For instance, the EM tree species of temperate Europe and North America have virtually no similarity (the genera, of course, are highly overlapping), but 27% of EM fungal species are common to both continents (using Sörenson's index). The genera of EM overlap by 100% on the two continents. We calculated this index value by comparing the EM species in fungal floras of the two continents (Phillips, 1981, 1991). This comparison must be made with some qualifications. These fungal floras are not comprehensive, as for instance virtually no hypogeous fungi are included in the fungal floras of Phillips (1981, 1991). In addition, some species that occur on both continents appear morphologically different and occur in different habitats even though they key out to the same species. An example is *Boletus satanus* of the moist beech forests of Europe, but in North America it occurs in semiarid to mesic oak woodlands of California and Oregon. Other EM fungi may actually be species complexes, such as *Laccaria bicolor*, *L. laccata* and *Russula emetica*, that occur on both continents but might actually be different species.

Second, only about 150 species of AM fungi have been identified (Schenck and Perez, 1990) but more than 5400 species of EM fungi have been reported (Molina et al., 1992) (Fig. 1). This compares with some 500,000 plant species. While many fungal species remain to be discovered, the ratio of AM to EM fungi is unlikely to increase. Only six genera of AM fungi are currently recognized, but more than 148 genera of EM fungi.

Third, the AM fungi display little specificity in their associations with host plants, while the EM fungi exhibit a wide range of specificity, from those that are specific to individual plant genera, to promiscuous fungi. Virtually any AM fungus can associate with any vascular plant that forms arbuscular mycorrhizae. Such broad AM associations can be experimentally observed in greenhouse pot cultures, where one fungal species per pot will associate with the available host plant. In the field the host may select a particular fungal species, as evidenced by different fungal species in the rhizosphere of different host species (Guo et al., 1993; Johnson et al., 1992; Nelson and Allen, 1993). Some EM fungi, on the other hand, are highly specific in their associations. The EM genera *Suillus*, *Rhizopogon*, *Leccinum*, *Brauniella*, *Gomphogaster*, and *Hydrangium* are 80-100% restricted to individual plant genera or families (Molina et al., 1992). For instance, *Hydrangium* is found only on *Eucalyptus*, while *Suillis* and *Rhizopogon* are restricted to the Pinaceae. On the other extreme are those fungi that associate with most

EM hosts, including such genera as *Amanita* and *Laccaria*. Most fungi tend to be intermediate in their host specificity, being associated with one or a few plant families (Molina et al., 1992).

Fourth, fungi can be perceived as macroorganisms rather than microorganisms because they form a mycelium, and the EM fungi form a more extensive mycelium than the AM fungi. The EM fungi belong primarily to the Basiomycotina and the Ascomycotina, which have anastomosing hyphae that have experimentally been shown to form extensive mycelia ranging tens of meters across a forest floor (Woods and Brock, 1964, and see review by Miller and Allen, 1992). These mycelia form a network of rhizomorphs that may act like the conducting tissue of plants. Since they cover such a large area, and may be specific to certain host plants, the EM fungi may be able to control the distribution of EM plant species to a certain degree. Typically a number of EM fungal species will coexist, forming multiple networks. Individual species of fungi may dominate patches of soil in some cases and associate with single tree species, or multiple species of EM fungi may coexist as mycobionts on one or a few tree species. Experimental evidence for fungal control of plant diversity is lacking, but inferential evidence comes when the fungi are destroyed, as by acid rain. Kowalski (1987) showed that the normal EM fungi are lost even before the coniferous trees die, and are replaced by other EM species that form a weak sheath. Although unidentified, these were not fungal species that could be found in unaffected stands. Thus the trees in this stand may well have been adversely affected because of a combination of acid rain and poor mycorrhizal functioning. This suggests that the normal EM fungi may be less tolerant of the acid soil environment than the trees or the replacement EM fungi, and the trees and different species of fungi each have their own environmental tolerance limits.

The AM fungi, by contrast, are in the more primitive Zygomycotina, specifically in the order Glomales (Morton, 1990), which do not have anastomosing hyphae. These fungi form a fan-like mycelium (Friese and Allen, 1991) in contrast to the net-like mycelium of most EM fungi. The AM mycelium is also much smaller in extent and finer than the EM mycelium, and lacks the visible rhizomorphs. The distance across an AM mycelium may be on the order of 1 m (Chiarello et al., 1982), which places it on the same order of magnitude as a single plant such as a shrub or small tree. There may be hyphal linkages among several host individuals, but it is unlikely these are as effective as EM rhizomorphs (Miller and Allen, 1992; Newman and Eason, 1993; Read, 1992). However, the AM fungi clearly lack the potential to control plant species diversity across large areas both because of their smaller hyphal networks and their lack of specificity. In a discontinuous AM hyphal network, there would be a greater potential for invasion by a diversity of plant species that could associate with any fungus. In a continuous EM hyphal network, only plants that are able to associate with specific fungal species could colonize. This network could contain one or many species of fungi, as long as a few fungi specific to certain plant species were abundant. Connell and Lowman (1989) also proposed that the extensive hyphal network of EM fungi may contol plant richness in tropical forests.

Based upon these four observations, we believe there is sufficient evidence to show that the type of mycorrhizal fungus, AM or EM, may regulate plant diversity. We next present information on patterns of plant diversity that will help to support this hypothesis. The ultimate proof may require experimentation, but we present this information in the spirit of opening up avenues for exploration.

Worldwide distribution patterns of AM and EM fungi and plant diversity

Moser (1967) produced a map of the distribution patterns of AM and EM forests worldwide that, with some updated information on recent surveys, still stands as a general pattern of distribution of these two predominant mycorrhizal types (Fig. 2). Basically, the EM forests include the boreal and temperate coniferous forests, the high elevation oak, pine, southern beech and coniferous forests in the tropics, subtropics, and mountain ranges of arid and semiarid regions, the *Eucalytus* forests of temperate Australia, and the tropical forests of Malaysia and northeastern Australia. The southeast Asian forests are actually mixed AM/EM (Janos, 1988), ranging from sites that are predominantly EM (Smits, 1983) to those that have only 10% EM roots (Riess and Rambell, 1980). Other tropical forests are predominantly or exclusively AM, including the South American, African and Indian moist and deciduous tropical forests. Even these may have some EM trees, such as Leguminosae in Africa and Dipterocarpaceae in India (Alexander and Högberg, 1986; Högberg, 1982; Janos, 1988; Newbury et al., 1988; Thoen and Ba, 1989) Moser (1967) and Meyer (1973) had shown deciduous tropical forest in Central Amer-

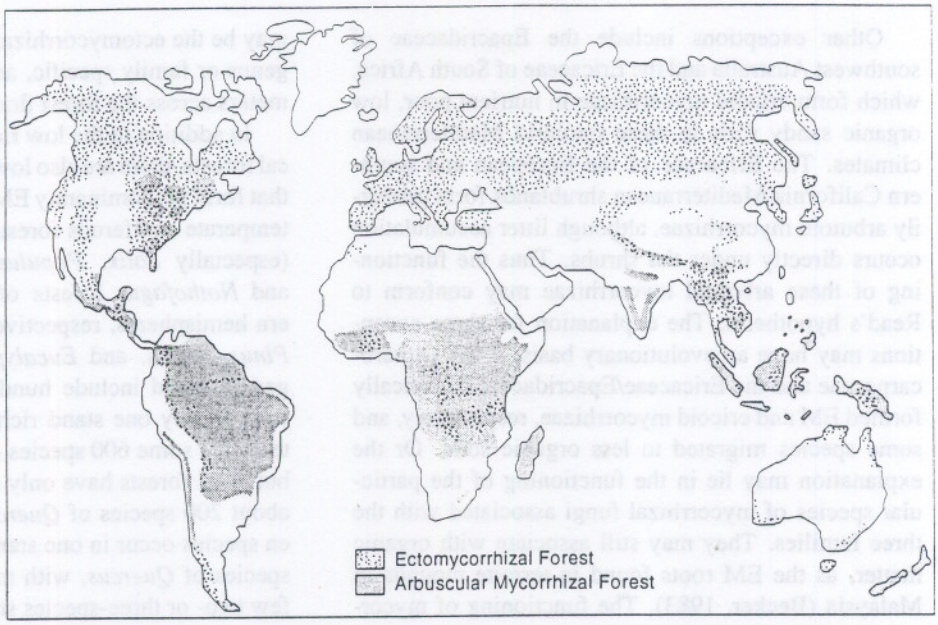

Fig. 2. Distribution of arbuscular mycorrhizal (AM) and ectomycorrhizal (EM) forests of the world. Modified from Moser (1967).

ica as EM, but it is very much an AM system (Janos, 1980), as is dry tropical forest in Africa (Högberg, 1992). Other AM forests occur in New Zealand, and in patches as mixed AM/EM forests in temperate climates. For instance, the AM genera *Fraxinus* and *Acer* are interspersed with EM Fagaceae and Pinaceae in eastern North America, the AM *Sequoiadendron gigantea* and *Calocedrus decurrans* are mixed with EM Pinaceae in the Sierra Nevada range of California, and the AM genera *Ulmus*, *Sorbus* and *Tilia* (the latter genus can be AM or EM), which were once abundant lowland forests in pre-agricultural Europe were interspersed with EM *Fagus* and Pinaceae.

While Moser's map only showed the mycorrhizae of forests, Read (1983) predicted where these and other mycorrhizal types should occur worldwide. The arid and semiarid regions of the world, where soil organic matter is low, typically have AM fungi, including the deserts, grasslands, and shrublands. Exceptions to these are savannas with scattered EM trees, such as the oak savannas of European and California Mediterranean regions, the pinyon pine woodlands of the Great Basin in the U.S. or the moist African savannas. EM trees are found more often in moist savanna, AM in dryer savanna (Högberg, 1989). The tundra regions, which are high in organic matter, have virtually no AM mycorrhizae (Bledsoe et al., 1990), but they do have short-statured EM genera such as Salicaceae and Ericaceae with ericoid mycorrhizae. In general, soils of high surface organic matter have EM and ericoid mycorrhizae. Read's (1983) hypothesis is based upon the ability of the different mycorrhizal types to utilize organic forms of nitrogen. The ericoid mycorrhizae that were studied in the British heathlands are best able to utilize organic nitrogen, with ectomycorrhizae also having this ability, but arbuscular mycorrhizae probably have limited or no ability to break down organic matter (Abuxinadah and Read, 1986; Leake and Read, 1990; Read, 1992; Read and Bajwa 1985; Read et al., 1985).

Read's (1983) hypothesis is appealing in its simplicity, but there are a number of exceptions. For instance, the Dipterocarpaceae-dominated tropical forests of southeast Asia have soils low in organic matter, even though they are largely ectomycorrhizal forests in some areas (Smits, 1992). However, the small scale patch dynamics of *Shorea*, a dipterocarp, indicates increased root proliferation in the organic soils of termite mounds (Becker, 1983). African EM trees are also associated with organic matter (Alexander, 1989), and they may be able to utilize organic forms of phosphorus and nitrogen directly (Newbery et al., 1988; Högberg, 1990). Alexander (1990) suggested that nutrient cycling in the soils under EM Leguminosae of Africa is more rapid than in nearby AM tree species.

Other exceptions include the Epacridaceae of southwest Australia and the Ericaceae of South Africa, which form ericoid mycorrhizae in nutrient poor, low organic sandy soils in these semiarid Mediterranean climates. The Ericaceae of the European and southern California Mediterranean shrublands form primarily arbutoid mycorrhizae, although litter accumulation occurs directly under the shrubs. Thus the functioning of these arbutoid mycorrhizae may conform to Read's hypothesis. The explanation for these exceptions may have an evolutionary basis, if the Dipterocarpaceae and the Ericaceae/Epacridaceae historically formed EM and ericoid mycorrhizae, respectively, and some species migrated to less organic soils. Or the explanation may lie in the functioning of the particular species of mycorrhizal fungi associated with the three families. They may still associate with organic matter, as the EM roots found in termite mounds in Malaysia (Becker, 1983). The functioning of mycorrhizae in mixed AM/EM forests is also of interest, as the partitioning of resources may be between fungi that are EM and can use organic nutrients, and those that are AM and are possibly more restricted to uptake of mineral nutrients.

The next step is to determine how EM and AM fungi relate plant diversity. This is best accomplished by focussing initially on forest biomes. Moist tropical forests are known for their high plant species richness, but patches and large stands occur within them that are low in richness and diversity (Alexander, 1989; Newbery et al., 1988; Connell and Lowman 1989). This curious occurrence of stands consists of single species tree dominants that occupy 80% or more of the trunk basal area. Connell and Lowman (1989) list a number of stands in forests throughout the tropics that have such dominance patterns, and suggest that the common denominator is that they are all ectomycorrhizal forests. In fact, some AM stands may also have low richness of trees (Alexander, 1989; Connell and Lowman 1989), but the overall pattern is striking. Many of the single species dominant forests occur in the extensive EM Dipterocarpaceae of southeast Asia and more limited stands in tropical Africa. This does not mean that the Dipterocarp forests are low in overall richness, as they are among the highest in plant species richness in the world (Ashton, 1988). However, their evenness is low in the stands dominated by a single tree species and their richness comes largely from the understory AM species. As suggested by Connell and Lowman (1989) and Alexander (1989), the reasons for the maintenance of low diversity tropical forest stands may be the ectomycorrhizal mycelium, which is often genus or family specific, and which can extend many meters across the forest floor.

In addition to the low richness/low evenness tropical forests, there are also low richness temperate forests that form predominantly EM. These include boreal and temperate coniferous forests, boreal deciduous forests (especially *Salix*, *Populus*, *Betula*, *Alnus*), *Fagus* and *Nothofagus* forests of the northern and southern hemispheres, respectively, *Quercus* and *Quercus-Pinus* forests, and *Eucalyptus* forests. Many of the genera listed include hundreds of species, but typically in any one stand richness is low. For instance, there are some 600 species of *Eucalyptus* in Australia, but most forests have only a few species. Mexico has about 200 species of *Quercus*, but no more than seven species occur in one stand, while California has 18 species of *Quercus*, with mainly single species and a few two- or three-species stands. Striking in their lack of tree richness are the extensive coniferous forests of the northern latitudes, that may be dominated throughout millions of ha by one species, such as *Pseudostuga menziesii* in North America or *Picea abies* in Europe. Low diversity in temperate and northern forests may also be maintained by EM fungi as in the tropics, but other mechanisms which restrict speciation in the colder and younger biomes also come into play.

The relationship between mycorrhizal type and plant species richness is presented as a hypothesis to be further tested. Just as with Read's (1983) hypothesis that relates soil organic matter and latitude to mycorrhizal type, we realize that there will be exceptions to our hypothesis. Such exceptions occur because mycorrhizae are but one of many factors that determine plant species richness (Table 1). But the worldwide pattern of this relationship is so strong, that it bears discussion and further research to understand the pattern and mechanisms.

Diversity of EM fungi

While the EM forests worldwide tend to be low in plant species diversity, the fungi themselves have rather high richness. The fungal floras of Europe and North America contain large numbers of EM species, but other continents have been less well explored. Hawksworth (1991) suggested that only 5% of the fungi have been discovered, but probably a much larger percentage of EM fungi have been discovered because they have macroscopic sporocarps. The microfungi are less well

Table 1. Richness of ectomycorrhizal fungi from different locations

Vegetation type	#Species	Area	Source
Jarrah Forest, SW Australia	90	?	Hilton et al. (1988)
Douglas Fir Forest, Oregon	100*	100 ha	Trappe and Molina (Unpubl.)
Douglas Fir Forest	2000*	WN. America	Trappe (1977)
Coniferous Forest	53	Kashmir	Watling and Abraham (1992)
Oak Woodland, Riverside Co., Ca	41	1 ha	M. Allen (Unpubl.)
Oak Woodland, S. Italy	40	1 ha	Dedominicis and Barluzzi (1983)
Oak-Pine Forest, Virginia	138	0.5 ha	Palmer et al. (1983)
Oak-Pine Forest, Mexico	67	N. Vera Cruz	Guzman (1980)
Glacial Forefront, S. Alaska	10	10 ha	Trappe et al. (Unpubl.)
Seasonal Tropical Forest, Senegal	44	?	Thoen and Ba (1989)

*Estimates.

described. Trappe (1977) estimated that as many as 2000 species of EM fungi may associate with Douglas fir throughout its range, which extends from the Rocky Mountains in the U.S. and Canada to the Sierra Nevada and northward into British Columbia (Table 1), but within any one stand of Douglas fir there may be 100 EM fungal species. This suggests there is relatively high between-stand, or beta diversity of the fungi, although not of the forest canopy. In other words, a uniform and relatively extensive plant community may support many different types of fungal communities. The understory plant diversity cannot explain the high EM diversity, because it is typically not as rich as the fungi, and most of the species are herbaceous AM or ericoid (e.g. Kovacic et al., 1984). Thus, as we hypothesized above, the fungi are locally adapted to the soils and climate, or there may be biogeographic limitations on their dispersal. The biogeographic argument may be true for some species of fungi, although not for all because many North American species are circumboreal.

EM fungal collections are difficult to compare because most were made for taxonomic rather than ecological purposes. Most accounts do not give the size of area sampled, the length of the sampling time, or the precipitation regime during sampling which is so important for sporocarp formation. We have compiled a list from the literature and from the authors to compare richness patterns (Table 1). The Jarrah forest of southwestern Australia is dominated by two *Eucalyptus* species (*E. marginata* and *E. calophylla*) which are the only EM species in the forest, but over 90 species of EM sporocarps were found (Hilton et al., 1988). Many of these could not be identified and are likely to be undescribed species. Similarly, an oak-pine forest in Virginia, U.S.A., had 93 described species but a total of 138 species, described plus undescribed (Palmer et al., 1993). Oak-pine forest in northern Vera Cruz in Mexico yielded 67 species (Guzmán, 1980), and Watling and Abraham (1992) found 53 EM species in coniferous forests in a number of mountainous regions of Kashmir. The Mexican and Kashmir surveys covered a much larger area than the other collections reported in Table 1, but their richness was equivalent or even lower. This points to the need for standardization, or at least reporting of size of survey areas and duration of sampling to make comparisons. The two Mediterranean oak woodlands from Italy and southern California had similar richness, and were both collected during two growing seasons in similarly sized stands. The southern California collection was made during two years of above average precipitation (M. Allen, unpubl.). The number of EM fungi was unexpectedly low in seasonal tropical forest from Senegal, but the area supported only two EM tree species. In addition this was the first attempt to identify the EM fungi of this area, many of which could be determined only to genus (Thoen and Ba, 1989). The glacial forefront in Alaska was expectedly low in fungal richness, but collections were made during July 1992, when August would be more conducive to sporocarp fruiting (Trappe, Helm and Allen unpubl.).

The data from Table 1 are insufficient to determine whether EM fungal richness increases with decreasing latitude, as for plant species. Such a gradient might be expected, for instance, in oak forests from western North America southward into Central America. Oak species richness is low in the north and high in the south, but we know little of EM fungal richness along this gradient. The oak-pine forests of Vera Cruz, Mexico (Guzmán, 1980) had more species of EM fungi than the oak forests of Italy or California, but a much larger area was surveyed in Vera Cruz. A comparison of the fungal flora of Vera Cruz with North American fungal floras (Arora, 1986; Miller, 1968) reveals that all of the 67 Vera Cruz fungal species but one also occur in the United States. There is also no evidence that tropical forests have more species of EM fungi than temperate forests, as Thoen and Ba (1989) found only 55 species in a forest in southern Senegal, and Alexander and Högberg (1986) observed that the degree of specificity between fungus and host was not greater in the tropics than temperate regions. The question of latitudinal trends in fungal diversity cannot be definitively answered until more survey data are available, and until the surveys are adjusted to unit area of land surveyed so comparisons can be made. However, the preliminary information we present here indicate that EM fungi are not necessarily more diverse in tropical than temperate latitudes, so a simple multiplication of fungal species richness of temperate areas will likely not represent their richness in the tropics, at least not for EM or for that matter AM fungi.

Comparison of native EM fungi on different continents is revealing. We made this comparison for genera and species of the three Mediterranean sites (Table 2), southern California, southern Italy, and southwestern Australia (Table 2). The overlap in genera was 36 to 56% among any two of the three sites, while the overlap in species was 0 to 9%, using Sörensen's index (Mueller-Dombois and Ellenberg, 1974). One species in common to Australia and California is *Hydrangeum carneum*, which was introduced to California and occurs only on *Eucalyptus*. What is most interesting is that the vegetation is similar in dominant genera between Italy and California, but the Australian site has no plant genera in common. In spite of this, the fungal genera are highly similar between the Australian and the other two sites. This suggests either that EM fungal speciation is slower than plant speciation, or that there has been continual genetic exchange worldwide among the fungi.

In another comparison, Trappe (unpubl.) has compiled regional lists of EM fungal genera from southern California, southern Italy, and southwestern Australia, including both epigeous (31 genera) and hypogeous (45 genera) fungi. These lists encompass several vegetation types within each region, not just exclusively Mediterranean woodlands as in Table 2. The Sorensen's index for epigeous fungal genera is 93% between California and Italy, but only 70% between California and Australia and 65% between Italy and Australia. For the hypogeous fungi the similarity is even lower. California and Italy overlap by 70%, whereas the overlap with Australia is only 19% and 22%, respectively. These data suggest that endemism at the generic level is relatively small for epigeous fungi, which disperse their spores by air, potentially over long distances. Hypogeous fungi, which depend on animal mycophagy for relatively short-distance dispersal, have evolved much higher endemism between northern and southern hemispheres. Evolution of hypogeous fungal genera from common ancestry in pangean populations evidently proceeded in largely different directions in Laurasia than in Gondwanaland, as is true also for host plants. More exchange between hemispheres was possible for the air-born spores of epigeous fungi than for either hypogeous fungi or host plants, perhaps accounting for the considerable overlap of epigeous genera between hemispheres as well as continents within hemispheres.

Diversity of AM fungi

A list of AM fungal richness (Table 3) was prepared as for EM fungi (Table 1), and the striking difference is that the species number is typically much lower. In a survey of 68 sites across the range of *Artemisia tridentata* ssp *tridentata*, we found 48 species of AM fungi (Allen and Allen, unpubl.). This range corresponds to that of Douglas fir, but the AM fungal richness is two orders of magnitude lower (Table 1). No one site contained more than a dozen species. Thus, both alpha and beta diversity (sensu Whittaker, 1975) are lower for AM than EM fungi. In a seasonal tropical forest on the Pacific Coast of Mexico (Biological Field Station of Chamela, University of Mexico), we have a preliminary estimate of 20–25 species of AM fungi, a large portion undescribed (Allen, Allen and Rincon, unpubl.). This stands in contrast to the more than 1000 vascular plant species that occur in the 2000 ha station (Lott, 1985 and unpubl.). Similarly low counts

Table 2. Comparison of genera and species of EM fungi from three Mediterranean woodlands and percent similarity using Sorensen's index. C = California, I = Italy, A = Australia. Data from Hilton et al. (1988; Australia), DeDominics and Barluzzi (1983; Italy), and M. F. Allen (unpubl.; California)

	Genera collected			Genera in common		
	California	Italy	Australia	C-I	C-A	I-A
Amanita	+	+	+	+	+	+
Austroboletus			+			
Boletellus			+			
Boletus	+	+	+	+	+	+
Cantharellus		+				
Cortinarius	+	+	+	+		+
Craterellus		+				
Cystangium			+			
Dermocybe		+	+			+
Desceola			+			
Entoloma		+				
Fischerula sp.	+					
Genea sp.	+					
Hebeloma		+	+			+
Hydnangium carneum	+		+		+	
Hydnellum		+				
Hydnotrya sp.	+					
Hydnotryopsis sp. *noy*	+					
Hydnum		+	+			+
Hygrocybe	+					
Hygrophorus	+	+	+	+	+	+
Hymenogaster sp.	+		+		+	
Hysterangium	+					
Inocybe	+	+	+	+	+	+
Laccaria	+	+	+	+	+	+
Lactarius	+	+	+	+	+	+
Leccinum		+				
Lyophyllum		+				
Paxillus			+			
Phellodon			+			
Phylloporus			+			
Pisolithus tinctorius	+		+		+	
Ramaria			+			
Russuia	+	+	+	+	+	+
Scleroderma sp.	+					
Sclerogaster sp.	+					
Terfezia sp	+					
Tricholoma		+	+			+
Tuber	+					
Zelleromyces			+			
Genera count	21	18	24	8	10	12
Sörensen's Index				0.36	0.44	0.56
Species count	47	49	90	4	3	0
Sörensen's Index				0.09	0.05	0

Table 3. Richness of arbuscular mycorrhizal fungi from different locations

Vegetation type	#Species	Area	Source
Artemisia/Atriplex Shrub-Steppe, Wy	12	1 ha	M. Allen., unpubl.
Artemisia tridentata	48*	W. N. Amer	Allen et al., unpubl.
Seasonal Tropical Forest, Mexico	20–25	10 ha	Allen et al., unpubl.
Successional Grassland, Minnesota	19	0.5 ha	Johnson et al., 1992
Shrubland/Woodland, Brazil	16	?	Sieverding, 1990
Shrubland/Woodland, Zaire	20	?	Sieverding, 1990
Shrubland/Woodland, Colombia	21	?	Sieverding, 1990
Terminalia spp. *Forest*	8	1 ha?	Wilson et al., 1992
Terminalia spp. *Plantation* (8 stands)	8–14/std	1 ha/std?	Wilson et al., 1992
Terminalia spp. *All Stands*	41	9 ha?	Wilson et al., 1992

*20 new species not found in keys.

come from tropical woodlands in Brazil, Zaire, and Columbia (Sieverding, 1990), although the *Terminalia* moist tropical forests, native and planted in Africa, had a total of 41 species in fewer than 10 ha (Wilson et al., 1992), almost as many as occurred in the entire range of *Artemisia tridentata*. This may suggest that tropical AM fungi are more diverse than temperate, but considering the rather low numbers from Sieverding's (1990, 1991) studies, no clear patterns can be deduced.

As for the EM fungi, the reporting of species richness for AM fungi depends upon the size of the area sampled, the length of sampling time, season sampled, and yearly variation in precipitation and temperature. In an *Artemisia-Atriplex* steppe in southwestern Wyoming, a total of 11 species were found in three years of sampling, with no fewer than 7 but no more than 10 in any one year (Table 4). Each year certain species did not sporulate, although it is uncertain how yearly climatic variation correlates with individual species. Two years had average precipitation, 1981 and 1987, when 7 species were found, and the year with 10 species had above average precipitation. Why *Sclerocystis rubiforme* appeared in 1987 and not the other years cannot be explained, and shows how little we still know about the ecology of these fungi.

Species counts are only a beginning to understanding diversity patterns. An examination of fungal community relationships with the host plant community is necessary to understand how the fungi respond to both the environment and the host plant. These relationships have been observed for AM fungi in the western United States. In the large scale survey of AM fungi of *Artemisia tridentata*, we (Allen and Allen, unpubl.) learned that any one site had as many as 17 species, but the largest number of sites had only 1–4 species (Fig. 3). A total of 48 species were found in the 68 sites examined, and 20 of these are undescribed (Schenck and Perez, 1990). The most frequent species was *Glomus aggregatum* with occurrence on 32 of the sites, but 20 of the 48 species were found on only one site (Fig. 4).

The species of AM fungi exhibited a latitudinal gradient of occurrence (Allen and Allen, unpubl.). There were distinct northern, central and southern communities of fungi with the two sites from the edge of the Mojave Desert resembling the central communities. These distinct communities were determined by the locations of individual species. For instance, *Glomus aggregatum* and *G. fasciculatum* occurred throughout the range of sagebrush, but *G. deserticola* was restricted to the central and southern portions of its range. *Scutellospora calospora* occurred along the western and northern portions of the range, while *Glomus mosseae* was southern and central in distribution. The distributions of other minor species (Allen and Allen, unpubl.) also contributed to the latitudinal gradient observed in the fungal communities.

The study indicates that AM fungi form their own specific community patterns regardless of the host plant, which was always *Artemisia tridentata*. The community and individual species of fungi are determined by local environmental conditions. *Artemisia tridentata* is a generalist along this environmental gradient, as were a few of the frequent species such as *Glomus aggregatum* and *G. fasciculatum*. However, most species of fungi were more restricted in their ranges. Interestingly, many of them crossed the two major north-south oriented mountain ranges, the Sierra Neva-

Table 4. Species of arbuscular mycorrhizal fungi from *Artemisia tridentata-Atriplex gardneri* shrub-steppe during three t=years

1981	1982	1987
Glomus mirocarpum	*G. microcarpum*	*G. microcarpum*
G. fasiculatum	*G. fasiculatum*	*G. fasiculatum*
G. macrocarpum	*G. macrocarpum*	*G. macrocarpum*
G. mosseae	*G. mosseae*	*G. mosseae*
G. occultum	*G. occultum*	*G. occultum*
G. gerdemannii	*G. gerdemannii*	
Entrophosporo spp.	*Entrophospora* spp.	
	G. pallidium	
	G. aggregatum	*G. aggregatum*
	G. flavisporum	
		Sclerocystis rubiformis
n = 7	n = 10	n = 7
	new = 3	new = 1

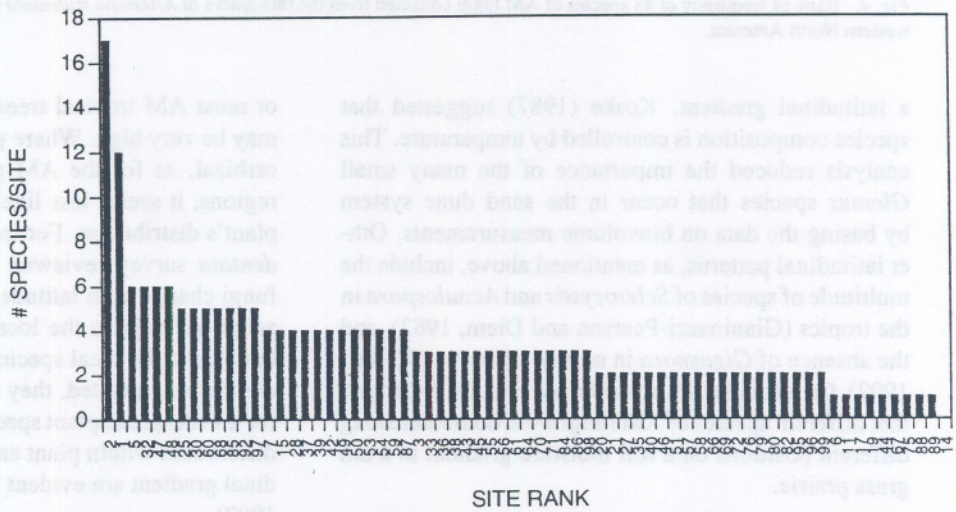

Fig. 3. Rank of richness of AM species collected from the rhizosphere of *Artemisia tridentata* spp. *tridentata* from 68 sites across western North America.

da and the Rocky Mountains. This may indicate that dispersal was not limiting, but rather that a north-south temperature or moisture gradient controlled their distribution. For other more localized species, local edaphic conditions may have played a role, as well as dispersal for some of the larger-spored species (Allen and Allen, 1992). Another consideration is that other species of host plants may control the fungal species. At any collection site, *A. tridentata* was in different types of plant communities and was associated with different neighboring plants. This included several coniferous species at the higher elevations, *Atriplex* and *Sarcobatus* in the saline lowlands, and *Artemisia*-steppe. Further analyses of the survey of *A. tridentata* mycorrhizae are underway. In a study on the effects of neighboring vegetation on AM species composition, Johnson et al. (1992) reported that species composition was highly controlled by the host plant. Thus, while AM fungi do not have the same degree of specificity that EM fungi have, they do show differences in relative abundances in the rhizospheres of different plant species.

Other studies on AM fungal distribution also show changes along environmental gradients. For instance, in an analysis of eight coastal sand dune sites along

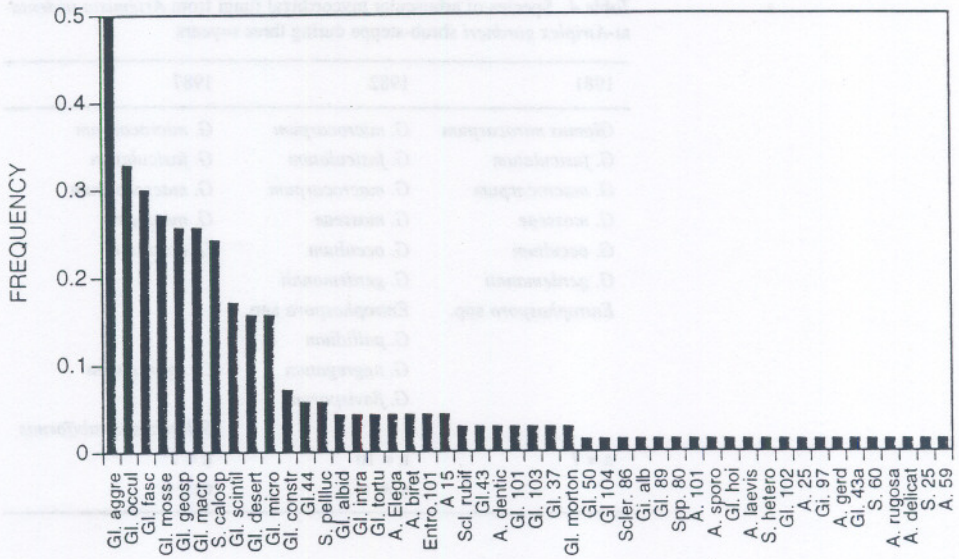

Fig. 4. Rank of frequency of 48 species of AM fungi collected from the rhizophere of *Artemisia tridentata* ssp. *tridentata* from 68 sites across western North America.

a latitudinal gradient, Koske (1987) suggested that species composition is controlled by temperature. This analysis reduced the importance of the many small *Glomus* species that occur in the sand dune system by basing the data on biovolume measurements. Other latitudinal patterns, as mentioned above, include the multitude of species of *Sclerocystis* and *Acaulospora* in the tropics (Gianinazzi-Pearson and Diem, 1982), and the absence of *Gigaspora* in northern Europe (Walker, 1992). On a smaller scale, Anderson et al. (1984) found that different species of AM fungi were dominant along different positions on a soil moisture gradient in a tall grass prairie.

Functional aspects of mycorrhizal diversity

We have suggested that the type of mycorrhizal fungi may affect the distribution and diversity of plants, and at the same time, the plants may control the local distribution of the fungi by associating or failing to associate with certain species. This suggests a "chicken and egg" situation where the mutualists are so closely interlinked that each controls the other's distribution to a certain extent. Again, each plant and fungal species has its individual response to the environment, and where they interact, they may affect each other to different degrees. Where the plants are obligately mycorrhizal, as for most EM woody plants worldwide and many or most AM tropical trees, the control by the fungus may be very high. Where plants are facultatively mycorrhizal, as for the AM plants of arid and semiarid regions, it seems less likely that the fungi control the plant's distribution. For instance, in the *Artemisia tridentata* survey reviewed above, the species of AM fungi change with latitude, and the plant species must adapt not only to the local environmental conditions but also to the local species of fungi. If the local fungi are the best adapted, they may be the best endophytes for a widespread plant species like *Artemisia*. Ecotypic differences within plant and fungal species on a latitudinal gradient are evident from field data (Allen et al., 1992).

In a transplant study of *Artemisia tridentata* and AM fungi between a central site (Reno, Nevada) and a southern site (eastern San Diego County), the plant growth responses showed highly specific responses to different species of mycorrhizal fungi. For instance, *Acaulospora elegans*, which occured in San Diego county but not in Reno, resulted in the greatest shrub volume of the Reno population at the Reno transplant sites, while *Scutellospora calospora* (transplanted from the Reno site) resulted in the smallest plants of both plant populations at both sites (Allen et al., 1992). Not only did different species of AM fungi cause different plant responses, but populations of the same fungal species, *Glomus deserticola*, produced different-sized shrubs within the same site (Allen et al., 1992 and

unpubl.). Similar results were found in physiological responses of *Agropyron smithii* to different populations of AM fungi, where the plants showed improved water relations from the fungal populations collected from droughtier soils (Stahl and Christensen, 1991; Stahl and Smith, 1984).

These results suggest that AM fungi have physiological diversity, even if they do not have high species diversity compared to the EM fungi. The two fungal types differ in their reproductive modes, which might explain the low diversity of AM fungi. AM fungi are thought to reproduce exclusively by asexual clamydospores, while EM fungi produce sexual spores. Both types, of course, proliferate via asexual hyphal vegetative growth. The individual clamydospores of AM fungi may have hundreds to thousands of nuclei, which have not been tested for genetic diversity (e.g., Wood and Cumming, 1992). If they are genetically different, they could provide an individual mycelium with the genome necessary to adapt to a wide variety of environmental conditions and plant hosts. We do not have any information on whether certain nuclei proliferate under certain conditions, or whether certain genes within the different nuclei are active under specified conditions. Answers to these questions may help us to understand why so few species have become so well adapted to so many different habitats.

Other observations suggest that there really are more than the few hundred potential species of AM fungi, because there are simply so few morphological characteristics upon which to differentiate the species. AM fungi are identified by spore morphology, color, number and thickness of wall layers, shape of hyphal attachment, and wall ornamentation (Morton, 1988). These are relatively few characteristics upon which to discriminate more than a few hundred species. Molecular techniques for differentiating spore types genetically may allow the discrimination of additional species.

Longevity of the two mycorrhizal types also does not explain their diversity differences. The AM fungi are much more primitive than EM fungi, having arisen with the first land plants during the Devonian (Kidstone and Lang, 1921), with identifiable modern characteristics by the Carboniferous (Stubblefield et al., 1987). EM fungi, by contrast, probably arose with the early angiosperms and gymnosperms during the Jurassic period, and proliferated during the Cretaceous to Tertiary (Pirozynsky, 1981). In spite of their great antiquity, AM fungi have not diversified morphologically as much as the EM fungi. A more likely explanation lies in the reproductive mode of the EM fungi, as sexual recombination and dikaryotization should have enabled much greater speciation than the AMs. In fact, there are a number of species of EMs that do reproduce primarily asexually, such as *Cenococcum geophilum* that reproduces primarily by vegetative sclerotia. Other species, including *Pisolithus tinctorius* and *Hebeloma* spp., also have sclerotia as important means of reproduction. Several of these have been identified from most or many continents, where they appear to be morphologically similar species. Of additional interest is that the EM species with narrow host range reproduce exclusively by sexual spores (Molina et al., 1992). Thus, in both the EM and AM types, asexual reproduction is related to broad host range and to broad geographical distribution.

Functional similarity of mycorrhizal fungi

All seven types of mycorrhizal fungi belong within one broad functional group, those that form a mutual symbiosis with living plants, but there are many species of mycorrhizal fungi in this broad group. This suggests some degree of functional "redundancy" as has been suggested for other microbial taxa as well as plants and animals (Tiedje et al., 1989). However, in assessing the notion of functional redundancy, it is important to recognize that the group contains species with highly diverse combinations of specific functions. The survey of AM fungi associated with *Artemisia tridentata* showed that some sites had very few species, and that these are probably locally adapted. Extinction of these species could cause measureable changes in the local flora, probably even where several species of AM fungi coexist. We have shown a seasonality of plant response to different AM fungal species, with some species causing maximum growth in spring, some in early summer, and some in late summer (Allen et al., 1992 and unpubl.). Loss of any one of these species might change the productivity of the system, as there are only a half dozen to a dozen species on any site within the sagebrush ecosystem. For instance, *Acaulospora elegans* sporulated only in the summer while other fungi sporulated in the spring, and plants inoculated with *A. elegans* had greatest growth responses in the summer, while other AM species produced greater growth responses in spring or early fall. Extinction of *A. elegans* on this site can be hypothesized to decrease overall productivity by reducing summer growth rates, a response that would be easily measureable. Thus for the functioning of mycorrhizae from the plant's point

of view, the fungi are likely dissimilar in ways we have not even begun to examine.

Although EM fungi are more diverse, there are two reasons why extinction of an EM fungal species might also produce a measureable effect on an ecosystem. First, many form highly specific associations with plant species that may be dominants of any particular system. The loss of these fungi would decrease the ability of their host plants to survive. Second, not all EM vegetation is associated with a highly diverse fungal flora, as for example the dozen or so species that colonize glacial till in southern Alaska (Table 1). The glacial till example may even form an outdoor laboratory for studying the effects of few species on plant growth, as unglaciated areas have more species (Trappe, Helm and Allen, unpubl. obs.). Other functions of EM as well as AM fungi need to be taken into account as well. For instance, they are important in the food web, constituting a higher fraction of the food consumption by many small mammals than plant material (Maser et al., 1988). In addition, they have different roles at different stages of succession. Some fungi that are infrequent in undisturbed ecosystems become abundant upon perturbation, so that there may be "early stage" and "late stage" fungi within any ecosystem.

Extinctions of fungi are likely taking place, as extinctions of plants are already known. Long term surveys of fungi in Europe have shown a decline in sporocarps of ectomycorrhizal species that is not matched by the lesser decline in saprophytic species (Fig. 5). While local extinction of these fungi cannot be proven until it is shown that their hyphae no longer exist in the soil, the downward trend is alarming. All of the causes for the decline is not known, but for some EM fungi the loss has been hypothesized to be caused by acid deposition (Arnolds, 1990; Kowalski, 1987). A data set on fungal diversity changes such as that of Arnolds (1990) could not be generated anywhere else in the world except Europe, where the macrofungi have long been studied. This points to the need for observing diversity patterns in other parts of the world, simply in an effort to understand what effects global change will have on the fungal mutualists that supply plants with nutrients. In some cases when a fungus is extirpated, other fungal species with similar functions will be available to colonize, suggesting that the term functional redundancy be replaced by the more accurate term functional similarity. We should be grateful that there are so many species that, even though they are similar (but not redundant) in their niches, perform similar, but not identical, functions. Human perturbations are causing species extinctions worldwide, but the extent to which mycorrhizal fungi are being lost is unknown. Hopefully they have high enough diversity and adaptability to the many environmental changes, that some will survive to prevent ecosystem collapse. However, ecosystem change is inevitable as mycorrhizal species are lost.

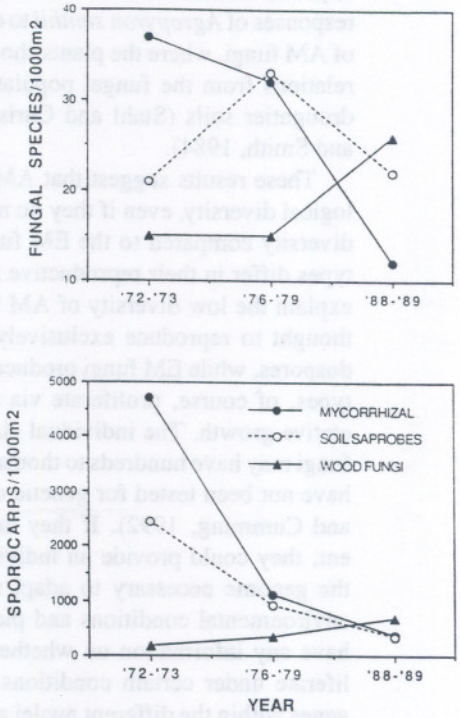

Fig. 5. Numbers of sporocarpic fungal species per 1000 m^2, and density of sporocarps per 1000 m^2, of three groups of fungi during three time periods. Data from Arnolds (1990).

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References

Abuzinadah R A and Read D J 1986 The role of proteins in the nitrogen nutrition of ectomycorrhizal plants. III. Protein utiliza-

tion by *Betula*, *Picea* and *Pinus* in mycorrhizal association with *Heboloma crustiliniforme*. New Phytol. 103, 507–514.

Alexander I J 1989 Mycorrhizas in tropical forests. *In* Mineral Nutrients in Tropical Forest and Savannah Ecosystems. pp 169–188. Ed. J Proctor. Blackwell Scientific Publications, Oxford, England.

Alexander I J and Högberg P 1986 Ectomycorrhizas of tropical angiospermous trees. New Phytol. 102, 541–549.

Allen M F 1991 The Ecology of Mycorrhizae. Cambridge University Press, Cambridge, England.

Allen M F and Allen E B 1992 Development of mycorrhizal patches in a successional arid ecosystem. *In* Mycorrhizas in Ecosystems. Eds. D J Read, A Fitter and I Alexander. pp 164–170. International Press, Oxford, England.

Allen M F, Clouse S D, Weinbaum B S, Jeakins S, Friese C F and Allen E B 1992 Mycorrhizae and the integration of scales: From molecules to ecosystems. *In* Mycorrhizal Functioning. Ed. M F Allen. pp 488–515. Chapman and Hall, New York.

Anderson R C, Liberta A E and Dickman L A 1984 Interaction of vascular plants and vesicular-arbuscular mycorrhizal fungi across a soil moisure-nutrient gradient. Oecologia (Berlin) 64, 111–117.

Arnolds E 1990 Mycologists and Nature Conservation. *In* Frontiers in Mycology. Ed. D L Hawksworth. pp 243–264. CAB International, Wallingford, UK.

Arora D 1986 Mushrooms Demystified. Second Edition. Ten Speed Press, Berkeley, California.

Ashton P 1988 Diptercarp biology as a window to the understanding of tropical forest structure. Annu. Rev. Ecol. Syst. 19, 347–370.

Becker P 1983 Ectomycorrhizae on *Shorea* (Dipterocarpaceae) seedlings in a lowland Malaysian rain forest. Malaysian For. 46, 146–170.

Bledsoe C, Klein P and Bliss L C 1990 A survey of mycorrhizal plants on Truelove Lowland, Devon Island, N.W.T., Canada. Can. J. Bot. 68, 1848–1856.

Chiarello N, Hickman J C and Mooney H A 1982 Endomycorrhizal role for interspecific transfer of phosphorus in a community of annual plants. Science 217, 941–943.

Connell J H and Lowman M D 1989 Low-diversity tropical rain forests: some possible mechanisms for their existence. Am. Nat. 134, 88–119.

DeDominicis V and Barluzzi C 1983 Ceonecological research on macrofungi in evergreen oak woods in the hills near Siena. Vegetatio 54, 177–187.

Egger K N and Sigler L 1993 Relatedness of the ericoid endophytes *Scytalidium vaccinii* and *Hymenoscyphus ericae* inferred from analysis of ribosomal DNA. Mycologia 85, 219–230.

Friese C F and Allen M F 1991 The spread of VA mycorrhizal fungal hyphae in the soil: inoculum type and external hyphal architecture. Mycologia 83, 409–418.

Gerdemann J W and Trappe J M 1974 The Endogone of the Pacific Northwest. Mycol. Mem. 5, 1–76.

Gianinazzi-Pearson V and Diem H G 1982 Endomycorrhizae in the tropics. *In* Microbiology of Tropical Soils and Plant Productivity. Eds. Y R Dommerques and H G Diem. pp 210–251. Dr. W. Junk Publishers, Dordrecht.

Guo B Z, An Z-Q, Hendrix J W and Dougherty C T 1993 Influence of a change from tall fescue to pearl millet or crabgrass on the mycorrhizal fungus community. Soil Sci. 155, 398–405.

Guzmán G 1980 Las especies de hongos micorrhizicos conocidos en la region de Uxpanapa-Coatzacoalcas-Los Tuxtlas-Papaloapan-Xalapa. Bol. Soc. Mex. Microbiol. 14, 27–38.

Harley J L and Smith S E 1983 Mycorrhizal Symbiosis. Academic Press, London.

Hawksworth D L 1991 The Biodiversity of Microorganisms and Invertebrates: Its Role in Sustainable Agriculture. CAB International, Wallingford, U.K.

Hilton R N, Malajczuk N and Pearce M H 1988 Larger fungi in the Jarrah forest: An ecological and taxonomic survey. *In* The Jarrah Forest: A Complex Mediterranean Ecosystem. Eds. B Dell, J J Havel and N Malajczuk. pp 89–110. Kluwer Academic Publishers, Dordrecht.

Högberg P 1982 Mycorrhizal associations in some woodland and forest trees and shrubs in Tanzania. New Phytol. 92, 407–415.

Högberg P 1989 Root symbioses of trees in savannas. *In* Mineral Nutrients in Tropical Forest and Savannah Ecosystems. Ed. J Proctor. pp 121–136. Blackwell Scientific Publications, Oxford, England.

Högberg P 1990 ^{15}N natural abundance as a possible marker of the ectomycorrhizal habit of trees in mixed African woodlands. New Phytol. 155, 483–486.

Högberg P 1992 Root symbioses of trees in African dry tropical forests. J. Veg. Sci. 3, 393–400.

Janos D P 1980 Mycorrhizae influence tropical succession. Biotropica 12, 56–64.

Janos D P 1988 Mycorrhiza applications in tropical forestry: are temperate-zone approaches approriate? *In* Trees and Mycorrhiza. Ed. F S P Ng. pp 133–188. Forest Research Institute, Kuala Lumpur, Malaysia.

Johnson N C, Tilman D and Wedin D 1992 Plant and soil controls on mycorrhizal fungal communities. Ecology 73, 2034–2042.

Kidstone R and Lang W H 1921 On the old red sandstone plants showing structure from the Rhynie chart bed Aberdeenshire. Part V. The thallophyte occurnng in the peat bed; the succession of plants through a vertical section of the bed and the conditions of accumulation and preservation of the deposit. Trans. Roy. Soc. Edinburgh 52, 855–902.

Koske R E 1987 Distribution of VA mycorrhizal fungi along a latitudinal temperature gradient. Mycologia 79, 55–68.

Kovacic D A, St John T V and Dyer M I 1984 Lack of vesicular-arbuscular mycorrhizal inoculum in a ponderosa pine *Pinus ponderosa* forest. Ecology 65, 1755–1759.

Kowalski S 1987 Mycotrophy of trees in converted stands remaining under strong pressure of industrial pollution. Angew. Bot. 61, 65–83.

Leake J R and Read D J 1990 The effects of phenolic compounds on nitrogen mobilisation by ericoid mycorrhizal systems. Agric. Ecosyst. Environ. 29, 225–236.

Lott E J 1985 Listados Floristicos de Mexico. III. La Estacion de Biologia Chamela, Jalisco. Herbario Nacional, Mexico City.

Malloch D W, Pirozynski K A and Raven P H 1980 Ecological and evolutionary significance of mycorrhizal symbioses in vascular plants (A Review). Proc. Natl. Acad. Sci. USA 77, 2113–2118.

Maser C, Maser Z and Molina R 1988 Small-mammal mycophagy in rangelands of central and southeastern Oregon. J. Range Manage. 41, 309–312.

Meyer F H 1973 Distribution of ectomycorrhizae in native and man-made forests. *In* Ectomycorrhizae: their ecology and physiology. Eds. G C Marks and T T Kozlowski. pp 79–105. Academic Press, New York.

Miller O K 1968 Mushrooms of North America. E.P. Dutton, Inc, New York.

Miller S L and Allen E B 1992 Mycorrhizae, nutrient translocation, and interactions between plants. *In* Mycorrhizal Functioning. Ed. M F Allen. pp 301–332. Chapman and Hall, New York.

Molina R, Massicotte H and Trappe J M 1992 Specificity phenomena in mycorrhizal symbiosis: Community-ecological consequences

and practical implications. *In* Mycorrhizal Functioning. Ed. M F Allen. pp 357–423. Chapman and Hall, New York.

Morton J B 1988 Taxonomy of VA mycorrhizal fungi: classification, nomenclature, and identification. Mycotaxon 23, 267–324.

Morton J B 1990 Evolutionary relationships among arbuscular mycorrhizal fungi in the Endogonaceae. Mycologia 82, 192–207.

Moser M 1967 Die ectotrophe Ernährungsweise an der Waldgrenze. Mitteilungen Forstl. Bundesversuchsanst. Wien 75, 357–380.

Mueller-Dombois D and Ellenberg H 1974 Aims and Methods of Vegetation Ecology. John Wiley and Sons, New York.

Nelson L L and Allen E B 1993 Restoration of *Stipa pulchra* grasslands: effects of mycorrhizae and competition from *Avena barbata*. Restor. Ecol. 1, 30–40.

Newbery D M, Alexander I J, Thomas D W and Gartlan J S 1988 Ectomycorrhizal rain-forest legumes and soil phosphorus in Korup National park, Cameroon. New Phytol. 109, 433–450.

Newman E I and Eason W R 1993 Rates of phosphorus transfer within and between ryegrass (*Lolium perenne*) plants. Funct. Ecol. 7, 242–248.

Palmer J G, Miller O K and Gruhn C 1993 Fruiting of ectomycorrhizal Basidiomycetes on unburned and prescribed-burned pine/hardwood plots after drought-breaking rainfalls in the Allegheny Mountains of southwestern Virginia. Mycorrhiza 4, 93–104.

Phillips R 1981 Mushrooms and Other Fungi of Great Britain and Europe. Pan Books, Ltd., London.

Phillips R 1991 Mushrooms of North America. Little, Brown and Co., Boston, Massachusetts.

Pianka E R 1966 Latitudinal gradients in species diversity. Am. Nat. 100, 65–75.

Pirozynski K A 1981 Interactions between fungi and plants through the ages. Can. J. Bot. 59, 1824–1827.

Read D J 1992 The mycorrhizal mycelium. *In* Mycorrhizal Functioning. Ed. M F Allen. pp 102–133. Chapman and Hall, London.

Read D J 1983 The biology of mycorrhiza in the Ericales. Can. J. Bot. 61, 985–1004.

Read D J and Bajwa R 1985 Some nutritional aspects of the biology of ericacious mycorrhizas. Proc. R. Soc. Edinburgh 85B, 317–332.

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

Riess S and Rambelli A 1980 Preliminary notes on mycorrhiza in a natural tropical rainforest. *In* Tropical Mycorrhiza Research. Ed. P Mikola. pp 143–145. Clarendon Press, Oxford, U.K.

Rosenzweig M L 1992 Species diversity gradients: we know more and less than we thought. J. Mammol. 73, 715–730.

Schenck N C and Perez Y 1990 Manual for the identification of VA mycorrhizal fungi Second Edition. International Culture Collection of VA Mycorrhizal Fungi, Gainesville, Florida.

Sieverding E 1990 Ecology of VAM fungi in tropical agroecosystems. Agric. Ecosyst. Environ. 29, 369–390.

Sieverding E 1991 Vesicular-Arbuscular Mycorrhiza Management in Tropical Ecosystems. Deutsche Gesellschaft für Technische Zusammenarbeit. Eschorn, Germany.

Smits W T M 1983 VIII. Dipterocarps and mycorrhiza, an ecological adaptation and a factor in forest regeneration. Flora Malesiana Bull. 36, 3926–3937.

Smits W T M 1992 Mycorrhizal studies in Dipterocarp forests in Indonesia. *In* Mycorrhizas in Ecosystems. Eds. D J Read, D H Lewis, A H Fitter and I J Alexander. pp 283–292. CAB International, Wallingford, U.K.

Stahl P D and Christensen M 1991 Population variation in the mycorrhizal fungus *Glomus mosseae*: breadth of environmental tolerance. Mycol. Res. 95, 300–307.

Stahl P O and Smith W K 1984 Effects of different geographic isolates of *Glomus* on the water relations of *Agropyron smithi*. Mycologia 86, 261–267.

Stubblefield S P, Taylor T N and Trappe J M 1987 Fossil mycorrhizae: a case for symbiosis. Science 237, 59–60.

Thoen D and Ba A M 1989 Ectomycorrhizas and putative ectomycorrhizal fungi of *Afzelia africana* Sm. and *Uapaca guineensis* Müll. Arg. in southern Senegal. New Phytol. 105, 549–559.

Tiedje J M, Colwell R K, Grossman Y C, Hodson R E, Lenski R E, Mack R N and Regal P J 1989 The planned introduction of genetically engineered microorganisms: ecological considerations and recommendations. Ecology 70, 298–315.

Trappe J M 1977 Selection of fungi for ectomycorrhizal inoculation in nurseries. Annu. Rev. Phytopath. 15, 203–222.

Walker C 1992 Systematics and taxonomy of the arbuscular endomycorrhizal fungi (Glomales)-a possible way forward. Agronomie 12, 887–897.

Watling R and Abraham S P 1992 Non-resupinate fungi of Kashmir forests: present knowledge. Mycorrhiza 2, 81–88.

Whittaker R H 1975 Communities and Ecosystems. MacMillan Publishing Co., New York.

Wilson J, Ingleby K, Mason P A, Ibrahim K and Lawson G J 1992 Long-term changes in vesicular-arbuscular mycorrhizal spore populations in *Terminalia* plantations in Cote d'Ivoire. *In* Mycorrhizas in Ecosystems. Eds. D J Read, D H Lewis, A H Fitter and I J Alexander. pp 268–275. CAB International, Wallingford, UK.

Wood T and Cummings B 1992 Biotechnology and the future of VAM commercialization. *In* Mycorrhizal Functioning. Ed. M F Allen. pp 468–487. Chapman and Hall, New York.

Woods F W and Brock K 1964 Interspecific transfer of ^{45}Ca and ^{32}P by root systems. Ecology 45, 886–889.