

Biodiversity of Mycorrhizal Fungi in Southern California¹

Michael F. Allen², Louise Egerton-Warburton, Kathleen K. Treseder, Cara Cario, Amy Lindahl, Jennifer Lansing, José Ignacio Querejeta, Ola Karen, Sharon Harney, and Thomas Zink

Abstract

Mycorrhizal fungi are a diverse group of organisms and form an integral link between plants and soil. These symbiotic fungi provide most of the soil resources to the plant in exchange for energy. However, their very diversity means that they can play many different roles and serve as indicators of changing ecosystem dynamics. There are probably more than a hundred mycorrhizal fungi associated with coast live oak alone in southern California. Data indicate that both the composition and functioning of these fungi change with the changing regional environment. Further, as regulators of ecosystem processes, changes in mycorrhizal composition and activity can ramify through the entire community. Understanding mycorrhizal and soil microbial dynamics and incorporating this understanding into management strategies will be crucial for sustaining viable preserves.

Key words: diversity, ecosystem, fungi, global change, mycorrhiza

Introduction

Biodiversity is a broad and general term used to describe the variety of organisms inhabiting a geographical or topological region of interest. For the most part, the emphasis of biodiversity focuses on listing or describing organisms of interest for protection or utilization, or the extent of this variation in terms of species number and abundance (Sisk and others 1994). However, there are vast arrays of organisms about which we know very little. According to recent estimates, we have described around 50 percent of vertebrates, but only 5 percent or less of insects and fungi (for example, Fröhlich and Hyde 1999, Hughes and others 2000). For prokaryotic organisms, we don't even know how to classify kingdoms, much less the concept of species. Of those we know, many are threatened with extinction, often before we even know who they are or their roles in ecosystems (Hughes and others 1997).

Fungi make a useful test group for understanding the concept of biodiversity and, in turn, understanding the environmental changes likely to affect the entire biota of a system (E. Allen and others 1995, M. Allen and others 1995). Fungi are found in every terrestrial environment and are directly and indirectly exposed to every perturbation. They range in scale from microfungi growing in solitary colonies on a single root tip to a macroorganism, such as *Hydnangium carneum*, that extends across an entire plant stand (Allen and others 1993). They also perform many

¹ An abbreviated version of this paper was presented at Planning for Biodiversity: Bringing Research and Management Together, a Symposium for the California South Coast Ecoregion, February 29-March 2, 2000, California State Polytechnic University, Pomona, CA.

² Center for Conservation Biology, University of California, Riverside, CA 92521-0334 (email address: michael.allen@ucr.edu)

essential roles in ecosystems, such as decomposing detritus and providing much of the nutrients needed by plants for photosynthesis. Thus, they are susceptible to every form of environmental change.

Of the vast array of fungi, mycorrhizal fungi represent a tractable group that is also sensitive to environmental perturbations. Mycorrhizae are mutualistic associations between plants and fungi that are localized within the root or root-like structures (Allen 1991). These fungi extend not only outward into the soil to extract nutrients and water, but they also extend into the plant roots where they exchange those resources for carbon. The only terrestrial plants not forming mycorrhizae are a limited number of weedy annuals in a few families such as the Chenopodiaceae or Cruciferae (Allen 1991). Thus, any environmental factor that affects plants can also affect these fungi. Likewise, each change in the substrate that could influence mycorrhizal fungi will also affect the host plants.

Mycorrhizal fungi are interesting and important in themselves. Many are commonly collected mushrooms for culinary purposes. They also make an important contribution to the diets of many mammals, especially rodents. Truffles are common, and searching for them is largely based on finding animal diggings. The hyphae of mycorrhizal fungi also provide much of the soil structure by producing glycoproteins called glomalin, which may make up as much as 25 percent of the soil organic matter and bind soil particles into macroaggregates (Rillig and others 1999, Treseder and others 2003). This structure protects nutrients and increases porosity and water-holding capacity. Finally, mycorrhizal fungi are responsible for much of the nutrient turnover and most of the transport dynamics that move resources around plants and between patches.

We have been studying mycorrhizal fungi in southern California vegetation types for over a decade. Such studies are vital because southern California is a designated hot spot for biodiversity conservation (Myers and others 2000), and the region is subject to intense perturbation from a variety of anthropogenic sources. Our observations have demonstrated some unique patterns (described below), but, of greater importance, they have indicated the need for long-term observations before definitive trends can be conclusively determined. We have focused on observations extending through precipitation cycles and across edaphic gradients at a variety of scales and on experiments evaluating responses to changing environments. Based on these data and the measured environmental change already observed by physical scientists, we believe that southern California ecosystems are likely beginning to undergo important and quantifiable change in microbial communities. Here, we focus on measurable responses of mycorrhizal fungi. These data can form a baseline against which future changes can be measured.

Mycorrhizal Fungi in Southern California: Biodiversity of a Group

Mycorrhizal fungi are diverse in southern California. Little is known about some key variables that would be involved in any program to describe and conserve biodiversity in mycorrhizal fungi. Although seven groups of mycorrhizal fungi are recognized, we focused largely on two major groups of mycorrhizal fungi. The first are ectomycorrhizal fungi found in symbiosis with coast live oak (*Quercus agrifolia*), pines, some other trees, and a few shrubs; ascomycetous and basidiomycetous fungi

form these mycorrhizae. The second are arbuscular mycorrhizal fungi (Glomales) associated with other trees, forbs, most shrubs, and grasses.

Structure of Diversity in Fungi

Diversity is richness and evenness of species, genomes, and functions. Fungi are different from higher plants and animals in that variation can occur and be measured within an individual as well as between individuals, populations, species, and clades. This variation can be detected at the scale of a small patch of ground (cm²) as well as at larger land units. Variation can also occur through time. As environmental pressures change, not only species but also the relative genetic composition of an “individual” mycelium can change.

Characterizing both the current and anticipated changes in fungal diversity with environmental perturbation is challenging. Fungi have multiple, haploid (1N) nuclei. In zygomycetous and glomalean fungi, no cross-walls exist. Thus, groups of nuclei can be found scattered throughout a developing mycelial fan. In ascomycetous and basidiomycetous fungi, most cells contain two separate 1N nuclei. The hyphae expand as individual cells multiply and elongate. However, when two compatible hyphae meet, they anastomose, forming a single mycelial network. As the mycelial network extends outward and multiple hyphae connect, a single connected “individual” mycelium can contain many different nuclei, and an individual connected hypha can contain cells with different functional and sometimes incompatible genes.

Ectomycorrhizal Fungal Diversity

Ectomycorrhizal (EM) fungi are a highly diverse group. Based on a decade of collecting from San Diego State University mycology classes, we have identified 74 species associated with coast live oak groves. Nevertheless, how diversity is characterized is as important as the data collection itself. To better evaluate this diversity, we have utilized a number of approaches. Because the real extent of demographic units in mycorrhizae is essentially unknown, as is the frequency of occurrence of metapopulations, we used geographically and ecologically stratified samples to evaluate patterns of both species and population diversity.

Our experimental research has been undertaken largely at Lopez Canyon, in the Western Riverside County Multispecies Reserve, and consists of evaluation of fungal diversity at the morphological and molecular level. Our first assessment was to plant oak seedlings in association with mature individuals (> 100 years old). At the end of the growing season, we harvested seedlings and estimated the number of morphotypes. Morphotypes are morphologically distinct mycorrhizal root tips that can be distinguished on the basis of characteristics such as texture, color, and hyphal types. Morphotypes sometimes correspond to fungal taxa, although there can be more than one fungal taxon per morphotype. Because of this ambiguity, we also employed molecular differentiation of tips that were morphologically similar. DNA was then extracted and amplified from roots of some seedlings using the polymerase chain reaction (PCR) of the internal transcriber region (ITS) of the small subunit of the ribosomal DNA. This part of the DNA chain was cut using endonuclease enzymes, leaving distinctive small units of DNA. These were run on gels that showed the size patterns of these DNA fragments, called *restriction fragment length polymorphisms* (RFLPs). These size units are distinctive to species and thus can be used to assess

diversity of mycorrhizal fungi at each individual root tip scale (Gardes and Bruns 1996, Karen and others 1997). RFLP comparisons allowed us to assess the numbers of actual mycorrhizal fungal taxa per tree based on the composition of the DNA.

During the winter rainy season of 2001, we found that the richness of EM morphotypes per seedling associated with mature coast live oak averaged 10; however, the richness at the stand level was expected to be much greater. There is considerable variability in the EM composition of seedlings from different oak patches resulting in much greater stand richness. Our initial findings showed that it was common for only a few EM morphotypes to be the dominant colonizers on an individual seedling. Furthermore, not only was there variability in the EM composition between seedlings from different patches, but also in which EM morphotypes were the dominant colonizers.

When we expanded to the RFLP analysis, a greater number of types emerged. For comparative purposes, an average of seven morphotypes per seedling were found, in contrast with an average of 12 RFLP taxa per seedling and a maximum of 20 RFLP taxa per seedling. The same pattern as morphotypes per stand emerged, though. A few dominant taxa could be found, with many infrequent species.

This finding is similar to EM community studies of pinyon pine (*Pinus edulis*) in Arizona (Gehring and others 1998) and New Mexico (Allen and others 2002). Pinyon pine trees act as isolated islands in which an individual tree has an average richness of 5 morphotypes but a stand of 8 trees has a richness of 20 to 30. Similarly, in coast live oak, only a few dominants per tree were found, but there was a great deal of variability among trees. As we sampled across the landscape, there was a continued replacement of species demonstrating a high level of β diversity (Allen and others 2002).

Our final effort was to investigate the diversity of species identified by sporocarps and the relationship between diversity and a stochastic measure of the rate of change in mycorrhizal diversity on a per area basis. At Camp Pendleton, we undertook a 4-year study monitoring the EM fungi fruiting in plots under stands of coast live oak and Engelmann oak. During this period, we identified 58 species of EM fungi. The species increment curve demonstrated a leveling off, suggesting that we had identified most of the sporulating fungi for those sites.

We estimated the land area for sampling, allowing us to calculate a z-value that describes the rate of change in diversity in relation to sample area size (from $s=ca^z$, where s is the number of species, or richness, c is a constant, and a is the area, Rosensweig 1995). Although we recognize that there are many means to assess diversity, the z-value is independent of size and allows comparisons to be made among habitats with varying areas. Since we are only able to assess mycorrhizal fungal responses to environmental change on small plots, this relationship provides some insights into how our region and mycorrhizal fungi might be affected.

Our results show that the z-value may be appropriate for comparison. For the individual seedling studies at Lopez Canyon, the z-value for root-tip morphotypes was 0.57 with an r^2 for the species area curve of 0.96. For the Camp Pendleton sporocarp assessment, the z-value was 0.58, with an r^2 of 0.975. These values are high compared with vertebrates, but they resemble the high values found in insect communities. Given that this z-value is high at the scales of patches and sites, then as the entire range of coast live oak is examined, the diversity of fungi has the potential to become extraordinarily high. This suggests that there probably are, in reality, up to

several hundred taxa associated with coast live oak alone, as has also been found for other mycorrhizal plants (Allen and others 1995, Sanders and others 1995, Sharples and others 2000,). Thus, the potential biodiversity of EM fungi and richness of valuable sources of genetic variation for a group of organisms important to the survival of this tree are extraordinary.

Chamise (*Adenostoma fasciculatum*) normally forms arbuscular mycorrhizae with all genera found in the region. However, during wet years (El Niño), we found EM associated with its roots and EM fungi in the stands (Allen and others 1999b). There was a high diversity of fungi ranging from *Cenococcum* and *Balsamia* spp. (ascomycetes) to a variety of basidiomycetes such as *Pisolithus* sp., *Cortinarius* spp., and *Hysterangium separabile*. We also found a new species of *Rhizopogon*: *R. mengei* (Allen and others 1999a). This is an important finding, since all other known species of *Rhizopogon* are associated with conifers. In addition, we sequenced the dominant fungus found on the root tips of chamise, and this fungus was an unknown species of ascomycete, most closely related to *Sarcocypha emarginata* (97 percent similarity in the sequence alignment of the 5.8S region, 63 percent similarity in ITS1, and 59 percent similarity in ITS2), a common fire-following fungus. There are clearly plant/fungal symbiotic combinations that we do not understand and have yet to explore.

Although we have focused on coast live oak and chamise, it must be noted that there are many other EM plants in southern California. These include all other species of oaks, all members of the Pinaceae, and chinquapin (*Chrysolepus semper-virens*). In our region, these never have been surveyed comprehensively.

Endomycorrhizal Fungal Diversity

Almost all other plants in southern California form endomycorrhizal associations. Most common is the arbuscular mycorrhizal (AM) type found in grasslands and shrublands. The fungal symbiont is a monophyletic group consisting of two distinct clades (phylogenetically-related species), the Glomaceae and the Gigasporaceae, which split with the earliest land plants (Redecker and others 2000, Morton and Redecker 2001). These different clades have some quite distinct characteristics important to mycorrhizal functioning and response to changing environments. Thus, while they are monophyletic, and species diversity is low (approximately 170 species are described worldwide), the different families diverged so long ago (350-400 million years) that functional differences have resulted (Hart and others 2001).

We conducted two relevant types of surveys. In the first, we examined the AM fungi associated with basin big sagebrush (*Artemisia tridentata* ssp. *tridentata*) throughout its distribution. This subspecies can be found throughout western North America, ranging north from Baja California in Mexico to British Columbia in Canada and eastward as far as North Dakota and New Mexico. Using this large spatial scale, we found that species richness of AM fungi increased with greater area sampled (*fig. 1*). However, most of the diversity of AM fungi associated with the Mojave ecotype of big basin sagebrush could be accounted for in just seven sites (*fig. 2*), because evenness actually declined as more sites were surveyed.

If we examine the pattern of distribution, there are several fungi—*Glomus aggregatum*, *Scutellospora calospora*, and *Paraglomus occultum*—that are widely distributed and found throughout the range. Others, such as *Sclerocystis rubiformis*,

Glomus tortuosum, *Archaeospora gerdemannii*, *Scutellospora pellucida*, and *S. heterogama*, are narrowly distributed, being found in only a few locations. In expanding to all 99 sites where basin big sagebrush exists, the total richness (number of AM fungal taxa) doubles, but the diversity continues to decline due to a lowered evenness. Clearly, each area has its specific combination of AM fungal species. The plant likely adapted to the local AM fungi but probably did not carry the AM fungi with it as it dispersed.

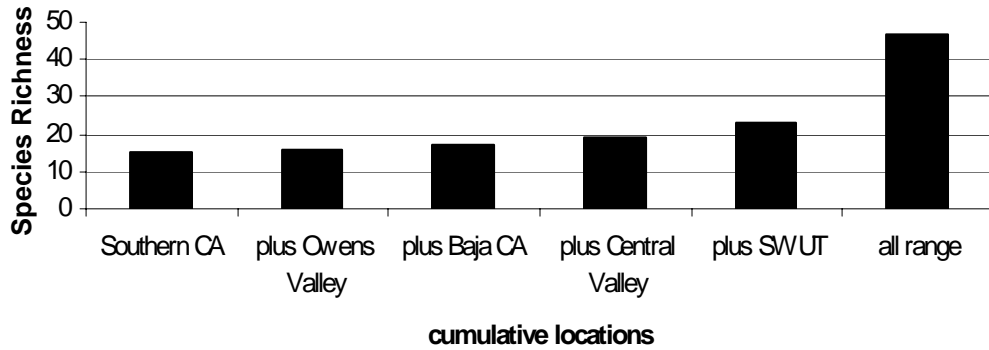


Figure 1—Richness of AM fungi associated with basin big sagebrush from southern California across its range into central California, Baja California, and across the Great Basin.

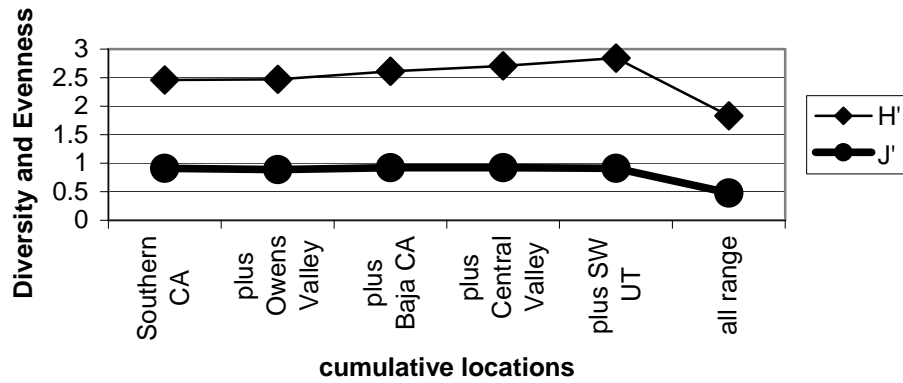


Figure 2—Diversity (H') and evenness (J') of AM fungi associated with basin big sagebrush from southern California expanding across its range into central California, Baja California, and across the Great Basin.

Just as importantly, the same genera and most of the same species diversity can be found associated with California sagebrush (*Artemisia californica*) and probably most other shrublands (Egerton-Warburton and Allen 2000). We do not yet have a large-scale sampling of AM fungi associated with forblands and only limited sampling in perennial *Stipa* grassland. However, in an undisturbed *Stipa* grassland, we found species of *Glomus*, *Acaulospora*, and *Scutellospora* (Allen unpublished data).

We know that, with few exceptions, AM fungi are not species-specific, but rather function as generalists and tend to infect whatever plant is nearby. We also know that there are growth responses that occur preferentially between specific combinations of plants and fungi (Klironomos and others 2000). This leads to increasing stand productivity and plant diversity in response to increasing AM fungal diversity (Klironomos and others 2000, van der Heijden and others 1998). However, the specific combinations that are crucial to a native plant community remain elusive.

Projections of Environmental Change: CO₂, N Pollution, Temperature, and Precipitation

Our global environment is changing dramatically and rapidly. This change translates to direct effects on our local environments and the need for retaining and managing for biodiversity on the remaining open space reserves. The clear changes are in atmospheric CO₂ and in NO₃ and NH₄ deposition. Less clear but potentially important are changes in temperature and precipitation (Rillig and others 2002).

CO₂ has risen dramatically since the industrial revolution, largely in response to increasing human demands for energy and increasing conversion of forest to agricultural lands globally (Houghton 1997). During the last ice age, atmospheric CO₂ was below 200 ppm (parts per million). By the beginning of the industrial revolution, atmospheric CO₂ was around 250 ppm. In the 1970s, it was up to 350 ppm and has rapidly increased, being currently about 370 ppm. Global projections range from 550 to 750 ppm over the next century. CO₂ has direct effects on plant dynamics in that the need for a C sink increases to handle the increasing fixation. Further, nutrients become more limiting to photosynthesis, especially N and P. Finally, with elevated CO₂, water-use efficiency rises.

Increased N deposition is also dramatic but concentrated at the regional rather than global scale. In southern California N largely comes from **denitrification** associated with dairy cattle and vehicular exhaust. Although the levels and forms are changing dramatically (see E. Allen and others, this volume), the amount remains important. Within the Los Angeles basin, deposition can range from 30 to 45 kg ha⁻¹y⁻¹, values equal to agricultural fertilization levels.

Temperature and precipitation changes are much less predictable. However, only small changes can have dramatic impacts. Further, these can remain within the bounds of evolutionary history and still affect the regional biota. According to most of the global circulation models (GCM), our region of southern California may be in the area of maximum climate and vegetation change (Watson and others 1997). Virtually every GCM shows increasing precipitation in southern California as a function of general warming caused by the greenhouse effect. With the heating of the oceans associated with the greenhouse effect, the model predicts increasing precipitation in a manner similar to the observed increases associated with El Niño phenomena. In this scenario, Neilson and colleagues (1998, and 2001 pers. comm.) note a significant increase in both winter and summer precipitation. This increase is coupled to increased water-use efficiency of desert plants associated with elevated CO₂. Consequently, their projections suggest that this increasing precipitation would result in increasing grasslands and mixed forest and decreasing shrublands and deserts.

Responses of Fungi to Change in Southern California

Although all of these projections fail to include all relevant processes, clearly there are enough indicators for us to be concerned with retaining our current biodiversity and managing for the diversity that can protect species of concern. Mycorrhizal fungi are only one group of organisms on which the ecosystem depends. Likely, there is more diversity in these fungi than absolutely required for oaks and similar critical species to survive. However, we are not very good at predicting which might be the crucial species. Below, we note some changes that we can see from our on-going experiments.

Diversity

Diversity and composition responded to changing perturbations. In experimental studies, the total amount of AM increased in response to elevated CO₂, and the increase was largely associated with the Gigasporaceae (Klironomos and others 1998, Treseder and others 2003; *fig. 3*). The amount of Glomaceae did not change even as CO₂ increased from 250 ppm to 650 ppm. At 750 ppm CO₂, the entire belowground system collapsed, and we do not understand the possible mechanisms. Conversely, in response to N deposition, sporulation in the Gigasporaceae disappeared, although some vegetative hyphae remained in association with roots (Egerton-Warburton and Allen 2000). However, the Glomaceae remained relatively constant; moreover, some species of *Glomus* increased in abundance following N enrichment. These findings indicate that N deposition promotes editing of the existing mycoflora, not an invasion. It should be remembered that AM fungi evolved during a period when atmospheric CO₂ was much higher than today (Allen 1996). CO₂ *per se* is not likely a detrimental factor for AM fungi. However, N has generally been the major limiting element in most terrestrial ecosystems, and N fertilization can have rather dramatic effects on AM fungal dynamics (see E. Allen and others, this volume).

There is little field experimental evidence on the interactions of CO₂ and N deposition and the composition of the AM fungal community. In the only data set to date, we find that there was a shift from the normal mix of AM fungi to the fine-endophyte form, *Glomus tenue* (Rillig and others 1999a). This may be a direct effect or a response to changing soil pH.

The abundance of ectomycorrhizae initially increased in response to N fertilization over a single growing season at Lopez Canyon. This area has not received long-term high levels of N deposition, as has the Los Angeles Basin. The z-values were 0.57, 0.68, and 0.60 (not significantly different) for control, N-fertilized, and weeded oak seedlings, respectively. In part, this demonstrates that in this region N remains the most limiting nutrient. N fertilization increased plant survival and growth, allowing a greater rate of both tip and EM formation. Also, these data demonstrate the need for long-term data on the effects of perturbations such as N deposition.

To our knowledge, no data on responses of EM fungal communities to elevated CO₂ have been published. This is important because increasing CO₂ could push ecosystems in high N depositional regions back to C/N equilibrium or propel the ecosystem along an entirely new trajectory.

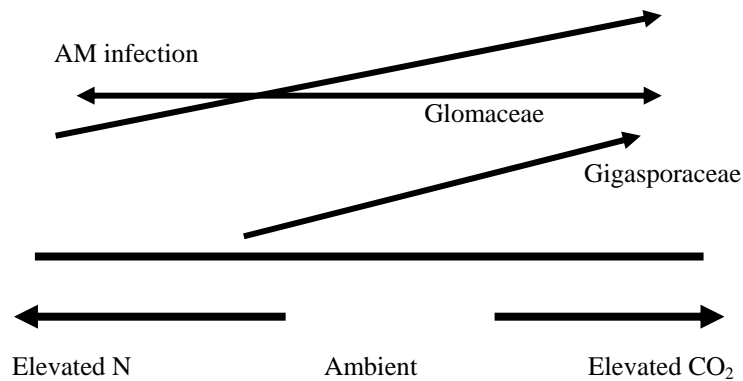


Figure 3—Changing AM activity along an atmospheric change gradient, ranging from elevated N (N deposition) to elevated CO₂. Data come from Egerton-Warburton and Allen (2000), Rillig and others (1999a), and Treseder and others (2003).

Mycorrhizal Activity

CO₂ and N have many impacts on mycorrhizal fungi and the functioning of soil ecosystems. CO₂ in particular has a very subtle effect on arbuscular mycorrhizae. In studies of newly disturbed soil, or pot cultures, AM fungi always appear to increase (Treseder and Allen 2000). However, in *in situ* studies, the total hyphal lengths per soil volume do not change (Allen in preparation). The hyphal lengths in soil aggregates and allocation of new C to soil via aggregates does increase as measured using both isotopic data and glomalin concentrations (Rillig and others 1999b, Treseder and others 2003). These data indicate that more C is allocated to mycorrhizae but that the turnover also increases. The residual C in the form of recalcitrant carbon builds up but probably not at the same rate as the increasing atmospheric levels that we are currently experiencing.

There are no data on the effects of elevated CO₂ on oak mycorrhizae from southern California. However, in a similar climate in Italy, ectomycorrhizal activity tends toward increasing cycling rates in a manner observed for AM (Cario and Allen in preparation).

N fertilization has mixed effects on total mycorrhizae. In N deficient situations, N fertilization can actually increase mycorrhizae. However, N can rapidly saturate shrublands and forb communities, causing a decline in the abundance of mycorrhizae often within three years following the onset of N enrichment (Egerton-Warburton and Allen 2000).

In forest ecosystems, there is a large capacity for absorbing N. We contrasted N cycling in oaks, comparing two sites: the first was the Sky Oaks Field Station, managed by San Diego State University, near Warner Springs, CA (N limited and low deposition); second was the San Dimas Experimental Forest (USDA Forest Service) (high deposition). The $\delta^{15}\text{N}$ data from San Dimas shows that N cycling has changed markedly since the experiment station was established in the 1930s. The values from San Dimas in 1935 (-2 percent) are equivalent to Sky Oaks, suggesting that Sky Oaks N-cycling patterns are less impacted by recent N deposition. Current leaf $\delta^{15}\text{N}$ is -4 percent. The values for the EM sporocarps for Sky Oaks and San Dimas average 6.9 percent and 6.8 percent, respectively. These data suggest that the

functioning of the mycorrhizal fungi (utilizing NH_4^+ and organic N) may not have changed but that depositional N is taken directly by the plant. In oak stands, initial evidence suggests that the oaks are not N saturated and mycorrhizal fungi remain active. How long this will persist and whether the fungal composition changes as the plants depend less on mycorrhizae for N are open questions.

Exotic Fungi

Pisolithus tinctorius is a widespread fungus associated with many host plants. Because it is so widespread, it was also widely used in reforestation efforts and in urban plantings (Marx and others 1984). (It is important to note that when this project began, it was considered a single species, but recent systematic studies are in the process of dividing *P. tinctorius* into several new species.) We studied the diversity of several sporocarps of *P. tinctorius*. Of relevance to us, this fungus is associated with oaks in California, pines in the southeastern US, and eucalyptus in Australia. We wanted to determine whether the fungus associated with cultivated trees was different from fungus associated with eucalyptus or from the native oaks.

On the basis of morphology, the sporocarps were virtually indistinguishable, and the spores ranged in size from 9.3 to 10.3 μm in diameter. However, the median spore diameter did vary significantly among the different isolates. The ITS region was also examined to determine whether the molecular structure could be distinguished. Even without further RFLP analyses it was possible to discern three ITS size categories: 610, 635, and 650 base pairs. When the spore size and ITS regions are examined together, the different sporocarps could be broken into six distinct groups (*table 1*). Importantly, there are four groups of sporocarps primarily found with exotic trees, two in the city of San Diego, one at the Santa Margarita Ecological Reserve (planted in 1974 as part of a biomass production study), and a third mixed planting near the Sky Oaks site with eucalyptus. There are two distinct genotypes found with native trees. The first was found in southern California with *Quercus agrifolia* and with *Q. turbinella* in New Mexico. This second is found in association with many native plants and stands scattered across California.

The important issue here is that there appear to be two native groupings and four likely introduced exotic fungi, which may switch hosts. Although we focused on *P. tinctorius*, there are many other exotic mycorrhizal fungi found in eucalyptus groves, including *Hydnangium separabile* from Tasmania, a fungus in the *Laccaria amethystina* group from Australia (Allen and others 1993). At this time, we do not know the implications of this invasion, but in other studies, switching can result in a less effective, or even detrimental, symbiosis for the plant.

Implications for Southern California Ecosystems

Mycorrhizal fungi are absolutely critical components of all terrestrial ecosystems in southern California and globally. These organisms provide the majority of nutrients to the plants, stabilize soils, sequester carbon, provide food for animals, and serve as the predominant microbial C sink for fixed photosynthate. They are extremely diverse with the differing fungi undertaking slightly different roles in the highly spatially variable semiarid to arid ecosystems of our region. Most global change models predict that our region will likely experience profound changes, potentially within our lifetimes.

Table 1—Differentiation of taxa of *Pisolithus tinctorius* from collections in Southern California based on spore size and ITS size fractions.

Group	Isolate	Host	ITS (bp)	Spore size (um)	Location
I	Pt 4	<i>Eucalyptus</i> sp.	610	9.3	SMER (Riverside County)
	Pt 2	<i>Eucalyptus</i> sp.	610	9.6	SMER (Riverside County)
	Pt 22	<i>Pinus radiata</i>	610	9.6	San Diego State University
II	Pt 16	<i>Eucalyptus</i> sp.	610	9.8	Sky Oaks (San Diego Co.)
	Pt 17	<i>Eucalyptus</i> sp.	610	9.8	Lake Skinner (Riverside Co.)
III	Pt 24	<i>Quercus turbinella</i>	635	9.2	Sevilleta LTER, NM
	Pt 7	<i>Quercus agrifolia</i>	635	9.4	Boden Field (Sky Oaks, San Diego Co.)
IV	Pt 23	<i>Eucalyptus</i> sp.	635	9.6	San Diego State University
V	Pt 11	<i>Quercus agrifolia</i>	635	9.7	Sky Oaks (San Diego Co.)
	Pt 1	<i>Chrysolepis sempervirens</i>	635	9.9	San Bernardino National Forest
	Pt 3	<i>Chrysolepis sempervirens</i>	635	9.9	San Bernardino National Forest
	Pt 6	<i>Chrysolepis sempervirens</i>	635	9.9	San Bernardino National Forest
	Pt 14	<i>Quercus agrifolia</i>	635	10	Sky Oaks (San Diego Co.)
	Pt 18	<i>Adenostoma fasciculatum</i>	635	10	Lake Skinner (Riverside Co.)
	Pt 10	<i>Quercus agrifolia</i>	635	10.1	Boden Field (Sky Oaks, San Diego Co.)
	Pt 13	<i>Quercus agrifolia</i>	635	10.3	Sky Oaks (San Diego Co.)
VI	Pt 19	<i>Eucalyptus</i> sp.	650	9.4	San Diego State University
	Pt 8	<i>Eucalyptus</i> sp.	650	9.6	SMER (Riverside County)
	Pt 15	<i>Quercus agrifolia</i>	650	9.6	Sky Oaks (San Diego Co.)
	Pt 20	<i>Eucalyptus</i> sp.	650	9.7	San Diego State University
	Pt 9	<i>Eucalyptus</i> sp.	650	9.9	SMER (Riverside County)
	Pt 21	<i>Eucalyptus</i> sp.	650	9.9	San Diego State University
	Pt 5	<i>Eucalyptus</i> sp.	650	10	SMER (Riverside County)
	Pt 12	<i>Quercus agrifolia</i>	650	10	Sky Oaks (San Diego Co.)

According to GCMs, our region generally will experience increasing precipitation (IPCC 1998). The impacts of this potential change can be seen in the effects of El Niño years on ecosystem dynamics. Moreover, the changing precipitation interacts non-linearly with N deposition, elevated CO₂, human population growth, and increasing development in many and complex ways. Our ability to manage the diversity and integrity of wildland ecosystems may depend on our understanding the microbial groups such as mycorrhizal fungi and sustaining their diverse and differing needs (Daily and others 2000).

Acknowledgments

These studies were funded by the National Science Foundation Biocomplexity and Ecosystem Studies Programs, the Shipley-Skinner Endowment Fund for the Multi-Species Habitat Reserve, and Camp Pendleton Marine Corps Base. We also thank the Base, San Diego State University, and the USDA Forest Service (San Dimas Experimental Forest) for permission to undertake much of this research.

References

- Allen, Edith B.; Allen, Michael F.; Helm, D.J.; Trappe, J.M.; Molina, Randy; Rincon, Emmanuel. 1995. **Patterns and regulation of arbuscular and ectomycorrhizal plant and fungal diversity.** *Plant and Soil* 170: 47-62.
- Allen, Michael F. 1991. **The ecology of mycorrhizae.** Cambridge: Cambridge University Press; 184 p.
- Allen, Michael F. 1996. **The ecology of arbuscular mycorrhizae: A look back into the 20th century and a peek into the 21st.** *Mycological Research* 100: 769-782.
- Allen, Michael F. 2000. **Mycorrhizae.** In: Alexander, M., editor. *Encyclopedia of Microbiology.* Second ed. San Diego: Academic Press; 328-336.
- Allen, Michael F.; Allen, Edith B.; Dahm, C.N.; Edwards, F.S. 1993. **Preservation of biological diversity in mycorrhizal fungi: Importance and human impacts.** In: Sundnes, G., editor. *International symposium on human impacts on self-recruiting populations.* Trondheim, Norway: The Royal Norwegian Academy of Sciences; 81-108.
- Allen, Michael F.; Lansing, Jennifer; Allen, Edith B. 2002. **The role of mycorrhizal fungi in composition and dynamics of plant communities: A scaling issue.** *Progress in Botany* 63: 344-367.
- Allen, Michael F.; Trappe, J.M.; Horton, T.R. 1999a. **NATS Truffle and truffle-like fungi 8: *Rhizopogon mengei* sp. nov. (Boletaceae, Basidiomycota).** *Mycotaxon* 70: 149-152.
- Allen, Michael F.; Egerton-Warburton, Louise B.; Allen, Edith B.; Karen, O. 1999b. **Mycorrhizae in *Adenostoma fasciculatum* Hook. & Arn.: a combination of unusual ecto- and endo-forms.** *Mycorrhiza* 8: 225-228.
- Allen, M.F.; Morris, S.J.; Edwards, F.S.; Allen, E.B. 1995. **Microbe-plant interactions in Mediterranean-type habitats: Shifts in fungal symbiotic and saprophytic functioning in response to global change.** In: Moreno, J.M.; Oechel, W.C., editors. *Global change and Mediterranean-type ecosystems.* Ecological Studies 117. New York: Springer Verlag; 287-305.
- Daily, Gretchen C.; Söderqvist, Tore; Aniyar, Sara; Arrow, Kenneth; Dasgupta, Partha; Ehrlich, Paul R.; Folke, Carl; Jansson, AnnMari; Jansson, Bengt-Owe; Kautsky, Nils; Levin, Simon; Lubchenco, Jane; Mäler, Karl-Göran; Simpson, David; Starrett, David; Tilman, David; Walker, Brian. 2000. **Ecology: The value of nature and the nature of value.** *Science* 289: 395-396.
- Egerton-Warburton, L.M.; Allen, E.B. 2000. **Shifts in arbuscular mycorrhizal communities along an anthropogenic nitrogen deposition gradient.** *Ecological Applications* 10: 484-496.
- Fröhlich, Jane; Hyde, Kevin D. 1999. **Biodiversity of palm fungi in the tropics: Are global fungal diversity estimates realistic?** *Biodiversity and Conservation* 8: 977- 1004.
- Gardes, M.; Bruns, T.D. 1996. **Community structure of ectomycorrhizal fungi in a *Pinus muricata* forest: Above- and below-ground views.** *Canadian Journal of Botany* 74(10): 1572-1583.

- Gehring, Catherine A.; Theimer, Tad C.; Witham, Thomas G.; Keim, Paul. 1998. **Ectomycorrhizal fungal community structure of pinyon pines growing in two environmental extremes.** *Ecology* 79(5): 1562-1572.
- Glass, N.L.; Kuldau, G.A. 1992. **Mating-type and vegetative incompatibility in filamentous ascomycetes.** *Annual Review of Phytopathology* 30: 201-224.
- Hart, M.M.; Reader, R.J.; Klironomos, J.N. 2001. **Life-history strategies of arbuscular mycorrhizal fungi in relation to their successional dynamics.** *Mycologia* 83: 1184-1196.
- Houghton, John T. 1997. **Global warming.** New York: Cambridge University Press; 251.
- Hughes, Jennifer B.; Daily, Gretchen C.; Ehrlich, Paul R. 1997. **Population diversity: Its extent and extinction.** *Science* 278: 689-692.
- Hughes, Jennifer B.; Daily, Gretchen C.; Ehrlich, Paul R. 2000. **Conservation of insect diversity: A habitat approach.** *Conservation Biology* 14: 1788-1797.
- Hughes, Jennifer B.; Roughgarden, Joan. 2000. **Species diversity and biomass stability.** *American Naturalist* 155: 618-627.
- Kårén, Ola; Högborg, Nils; Dahlberg, Anders; Jonsson, Lena; Nylund, Jan-Erik. 1997. **Inter- and intraspecific variation in the ITS region of rDNA of ectomycorrhizal fungi in Fennoscandia as detected by endonuclease analysis.** *New Phytologist* 136: 313-325.
- Klironomos, John N.; McCune, Jenny; Hart, Miranda; Neville, John. 2000. **The influence of arbuscular mycorrhizae on the relationship between plant diversity and productivity.** *Ecology Letters* 3: 137-141.
- Klironomos, John N.; Ursic, Margot; Rillig, Matthias; Allen, Michael F. 1998. **Interspecific differences in the response of arbuscular mycorrhizal fungi to *Artemisia tridentata* grown under elevated atmospheric CO₂.** *New Phytologist* 138: 599-605.
- Leslie, John F.; Zeller, Kurt A. 1996. **Heterokaryon incompatibility in fungi: More than just another way to die.** *Journal of Genetics* 75: 415-424.
- Loubradou, Gabriel; Turcq, Béatrice. 2000. **Vegetative incompatibility in filamentous fungi: A roundabout way of understanding the phenomenon.** *Research in Microbiology* 151: 239-245.
- Marx, D.H.; Cordell, C.E.; Kenney, D.S.; Mexal, J.G.; Artman, J.G.; Riffle, J.W.; Molina, R.J. 1984. **Commercial vegetative development of *Pisolithus tinctorius* and inoculation techniques for development of ectomycorrhizae on bare-root seedlings.** *Forest Science Monographs* 25: 1-101.
- Morton, J.B.; Redecker, D. 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.
- Myers, Norman; Mittermeier, Russell A.; Mittermeier, Cristina G.; da Fonseca, Gustavo A.B.; Kent, Jennifer. 2000. **Biodiversity hotspots for conservation priorities.** *Nature* 403: 853-858.
- Neilson, R.P.; Prentice, I.C.; Smith, B.; Kittel, T.G.F.; Viner, D. 1998. **Simulated changes in vegetation distribution under global warming.** In: Watson, R.T.; Zinyowera, M.C.; Moss, R.H.; Dokken, D.J., editors. *The regional impacts of climate change: An assessment of vulnerability. A special report of the Intergovernmental Panel on Climate Change Working Group II.* Cambridge: Cambridge University Press; 439-456.
- Redecker, Dirk; Morton, Joseph, B.; Bruns, Thomas D. 2000. **Ancestral lineages of arbuscular mycorrhizal fungi (Glomales).** *Molecular Phylogenetics and Evolution* 14: 276-284.

- Rillig M.C.; Treseder, K.K.; Allen, M.F. 2002. **Global change and mycorrhizal fungi**. In: van der Heijden, M.G.A.; Sanders, I.R., editors. Ecological Studies. Mycorrhizal Ecology. Berlin, New York: Springer-Verlag; 135-160.
- Rillig, Matthias C.; Allen, Michael F.; Klironomos, John N.; Chiariello, Nona R.; Field, Christopher B. 1998. **Plant-species specific changes in root-inhabiting fungi in a California annual grassland: Responses to elevated CO₂ and nutrients**. *Oecologia* 113: 252-259.
- Rillig, Matthias C.; Field, Christopher B.; Allen, Michael F. 1999a. **Soil biota responses to long-term atmospheric CO₂ enrichment in two California annual grasslands**. *Oecologia* 119: 572-577.
- Rillig, Matthias C.; Wright, Sara E.; Allen, Michael F.; Field, Christopher B. 1999b. **Rise in carbon dioxide changes soil structure**. *Nature* 400: 628.
- Rosensweig, Michael L. 1995. **Species diversity in space and time**. New York: Cambridge University Press; 458 p.
- Sanders, Ian R.; Alt, Monica; Groppe, Kathleen.; Boller, Thomas; Wiemken, Andres. 1995. **Identification of ribosomal DNA polymorphisms among and within spores of the Glomales: Application to studies on the genetic diversity of arbuscular mycorrhizal communities**. *New Phytologist* 130: 419- 427.
- Sharples, J.M.; Chambers, S.M.; Meharg, A.A.; Cairney, J.W.G. 2000. **Genetic diversity of root-associated fungal endophytes from *Calluna vulgaris* at contrasting field sites**. *New Phytologist* 148: 153-162.
- Sisk, Thomas D.; Launer, Alan E.; Switky, Kathy R.; Ehrlich, Paul R. 1994. **Identifying extinction threats: Global analyses of the distribution of biodiversity and the expansion of the human enterprise**. *Bioscience* 44: 592-604.
- Tilman, David. 1996. **Biodiversity: population versus ecosystem stability**. *Ecology* 77: 350-363.
- Treseder, Kathleen K.; Allen, Michael F. 2000. **The role of mycorrhizal fungi in soil carbon storage under elevated CO₂ and nitrogen deposition**. *New Phytologist* 147: 189-200.
- Treseder, Kathleen K.; Egerton-Warburton, Louise M.; Allen, Michael F.; Cheng, Yufu; Oechel, Walter, C. 2003. **Alteration of soil carbon pools and communities of mycorrhizal fungi in chaparral exposed to elevated carbon dioxide**. *Ecosystems* 6(8): 786-796.
- Van der Heijden, Marcel G.A.; Klironomos, John N.; Ursic, Margot; Moutoglis, Peter; Streitwolf-Engle, Ruth; Boller, Thomas; Wiemken, Andres; Sanders, Ian R. 1998. **Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability, and productivity**. *Nature* 396: 69-72.
- Watson, Robert T.; Zinyowera, Marufu C.; Moss, Richard H., editors. 1997. **The regional impacts of climate change: An assessment of vulnerability**. A Special Report of IPCC Working Group II. Cambridge: Cambridge University Press; 517p. IPCC = Intergovernmental Panel on Climate Change