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## Mycorrhizas take root at the Ecological Society of America

### Mycorrhizal ecology and related sessions at the Ecological Society of America (ESA) 92nd Annual Meeting, San Jose, CA, USA, August 2007

Mycorrhizal symbioses play an important role in virtually all terrestrial ecosystems (Smith & Read, 1997). They are known to have significant impacts on carbon and nutrient

cycling, soil formation and structure, plant productivity and diversity, and food web dynamics (Van der Heijden & Sanders, 2002). Although the importance of mycorrhizas is widely recognized, the study of these symbioses has historically been divided between two groups of scientists. Ecologists interested in this topic have mainly focused on the above-ground part of the symbiosis (i.e. the plants) and treated the below-ground part of it (i.e. the fungi) largely as a 'black box'. In contrast, mycologists have primarily focused on the fungi themselves and given less attention to the way in which these symbioses affect plants and other organisms. Despite their common interest, a look at the early mycorrhizal literature would indicate that ecologists and mycologists rarely interacted with each other. The division between these two groups, however, appears to be quickly disappearing. This was most recently evidenced at this year's Ecological Society of America (ESA) meeting in San Jose, CA, USA, where a record amount of research on mycorrhizal symbioses was presented. Four oral sessions and a poster session were devoted entirely to mycorrhizal ecology. More significantly, research involving the symbiosis was included in 23 different general sessions and made appearances in many talks devoted to other topics. The meeting was also the first gathering for the Fungal Environmental Sampling and Informatics Network (FESIN: <http://www.bio.utk.edu/fesin/>), which will have alternating meetings over the next 4 yr between ESA and the Mycological Society of America in order to bring these two groups of scientists closer together. Here we summarize a few of the highlights of the mycorrhizal work that was reported at the meeting.

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*'... researchers are increasingly finding new and innovative ways to test questions about mycorrhizal fungi under ecologically realistic conditions.'*

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### Molecular techniques

One fundamental aspect of ecological studies is the ability to identify the number of species present in a given area or sample. Because the active part of the mycorrhizal symbiosis occurs below-ground, researchers have increasingly relied on molecular techniques to assess the number of fungal species in their studies (Horton & Bruns, 2001). While the methods themselves have typically held center stage in research on mycorrhizal assemblages, this year's meeting showed that they have largely become second nature and the focus has shifted to how these techniques can be applied to

address broader ecological questions. For example, Shannon Schechter (University of California, Berkeley, USA) used a cloning and sequencing approach to compare the arbuscular mycorrhizal (AM) fungi associated with serpentine and nonserpentine ecotypes of *Collinsia sparsiflora* growing in adjacent plots. She found major differences in AM assemblage structure between the two ecotypes, suggesting that AM fungi may play a key role in plant adaptation to extreme soil environments. Jeri Parrent (Swedish Agricultural University, Sweden) examined the ectomycorrhizal (EM) root tip and hyphal assemblages in the Free Air Carbon Enrichment (FACE) plots in Duke forest, NC, USA and showed that increased carbon dioxide concentrations significantly shifted EM assemblage composition (Parrent *et al.*, 2006). Interestingly, many of the dominant fungi had different patterns of root tip to hyphal ratios between treatments, indicating that the assemblage shift may have important functional consequences in host plant response to global change. Working in three temperate hardwood forests in north-eastern Michigan, Ivan Edwards (University of Michigan, USA) found a strong spatial stratification of saprotrophic and EM fungi in soil litter and mineral soil horizons and showed that EM mycelium dominated the soil even in an *Acer/Tilia* forest where *A. saccharum*, the main dominant tree, is an AM associate. These studies, as well as many others presented at the meeting, demonstrate that the doors initially unlocked by molecular techniques are now open, providing significant insight into the ecological role of this symbiosis.

While molecular identification techniques have allowed mycorrhizal researchers to ask more ecologically based research questions, they have also revealed the high species richness of mycorrhizal assemblages (Dahlberg, 2001). The richness of these assemblages is often on the same order as that of the richest plant and animal assemblages and can be particularly high in areas with multiple host species (Ishida *et al.*, 2007). Our perceptions of mycorrhizal species richness are, however, strongly affected by sampling strategy (Horton & Bruns, 2001; Taylor, 2002). Lee Taylor (University of Alaska, Fairbanks, USA) provided another example of the domination of EM fungal mycelium in forest soil; this pattern has now been seen across an impressive array of northern temperate forest types (O'Brien *et al.*, 2005; Lindahl *et al.*, 2007; Ivan Edwards, this meeting). In addition, he showed that sampling fungal assemblages to saturation (i.e. capturing all of the species present in a given sample) can be challenging even in forests dominated by a single EM host species. Using a cloning and sequencing approach, he compared the diversity of fungal taxa found in 99 *Picea mariana* litter samples (380 clones) with that of one *P. mariana* litter sample (1080 clones). He found that, in both cases, the species–effort curves had still not plateaued and that approximately 50 fungal taxa were present in a 0.25-g soil sample! Interestingly, even some of the most common

sequence types within the single sample were not recovered again in the pooled sample that included it. This inability to saturate fungal collecting curves has been previously seen in root-tip surveys (reviewed in Horton & Bruns, 2001) and in a clone pool study of Duke forest soil (O'Brien *et al.*, 2005). In fact, the only cases in which saturation has been clearly achieved are those where only EM fungi were targeted, the forest was young, and the spatial scale was relatively small (Horton & Bruns, 2001; Peay *et al.*, 2007).

### Top-down vs bottom-up trophic interactions

Another factor bringing research on mycorrhizal fungi into the ecological mainstream is their integration into topics that have long interested ecologists. One of the classic debates in ecology has been about the relative importance of top-down vs bottom-up control of trophic interactions (see special feature articles in *Ecology* 73(3)). Although a sizable literature has developed on this topic, the role of mycorrhizal fungi has largely been overlooked. Working in Canadian grassland, J. C. Cahill (University of Alberta, Canada) examined the effects of AM fungi on plant–pollinator interactions. He found a strong bottom-up effect on pollinator community composition, with a 67% reduction in bumble bee visits in plots where mycorrhizal fungi were removed with benomyl. Conversely, in a semiarid woodland, Kitty Gehring (Northern Arizona University, USA) showed that parasitism (from mistletoe), competition (from other trees), and herbivory (from scale insects) on plants all have major independent top-down effects on EM assemblage structure. Interestingly, the EM assemblages of stressed plants converged on a core group of Pezizalean ascomycetes. Working in the same system, Chris Stultze (Northern Arizona University, USA) followed up on the differences in EM assemblages between pines that are resistant or susceptible to the pitch mass borer, *Dioryctria ponderosae*, and showed that, even if the insect was experimentally removed for many years, susceptible and resistant trees continued to show distinct assemblages. Even more surprisingly, he showed the same pattern for seedlings of resistant and susceptible trees, which indicated that the differences were driven at least in part by host genetics. Studies such as these clearly indicate that mycorrhizal fungi both affect and are affected by organisms at other trophic levels. Like the classic lynx–hare dynamics that are now realized to be influenced by additional trophic interactions (Krebs *et al.*, 1995), the increased inclusion of mycorrhizal fungi in ecological studies will clearly lead to a fuller understanding of the factors that control multitrophic dynamics.

### Models and manipulative experiments

Mycorrhizal researchers are also increasingly interested in using tools developed by ecologists and testing ecological

theories developed for other organisms on fungi. Modeling, for example, has long been used in ecology to generate predictions that can then be tested with empirical studies. Miroslav Kimmel (Colorado College, USA) presented a set of biological market models examining the optimal number of fungal symbionts with which a plant should associate (Kimmel & Salant, 2006). He found that the shape of the carbon–nitrogen trading curve (i.e. whether it is concave or convex) is likely to play a determining role in whether a plant will associate with one or multiple fungi. Many talks also showed the increased use of manipulative experiments to test the types of questions generated by models or correlation-based studies. Using a split-root experimental design, Jim Bever (Indiana University, USA) demonstrated that plants are able to differentially reward fungal symbionts that provide the most nutrients, but this reward system is apparently effective only in spatially structured environments. In a uniform pot setting, negative feedback dominates; that is, the worst fungal symbiont from the plant's perspective has a competitive advantage. This may be attributable to difference in scale between the fungal and plant partners. If a plant is not actually rewarding the best fungus directly, but rather is investing more in the most nutrient-rich part of its root system, then, when different fungi are intermingled at fine scales, the plant may not be able to direct rewards to the best symbiont and the fungus that provides little may reap a disproportionate reward for its limited effort.

Competition among mycorrhizal fungi was also the focus of P. Kennedy's talk (Lewis and Clark College, CA, USA). Manipulative laboratory and field experiments on a set of four EM fungi in the genus *Rhizopogon* showed that, when these fungi compete for colonization of pine seedling roots, timing, host root density, and inoculum type all matter. Differences in the speed of spore germination had been previously demonstrated to be a major determinant in competition between two of these *Rhizopogon* species (Kennedy & Bruns, 2005). Such 'priority effects' are well known in other organisms (Keddy, 2001) and are based on one competitor capturing a resource and making it unavailable to a second. New experiments showed that this was a general property among three of the *Rhizopogon* species, and that when order of colonization was artificially manipulated outcomes could be reversed. Although there are still significant challenges to manipulating mycorrhizal assemblages in the same way as those of other organisms, particularly in field settings, researchers are increasingly finding new and innovative ways to test questions about mycorrhizal fungi under ecologically realistic conditions (see Nara (2006) for an interesting lab–field hybrid example).

### Future advances

The most interesting advance in methods reported at the meeting was the use of 'quantum dots' by Matthew

Whiteside and Kathleen Tresender (University of California, Irvine, USA) to examine fungal uptake and transport of organic nitrogen sources. Selected amino acids or chitosan were bound to fluorescent nanoparticles and used to show that AM fungi were capable of uptake and transport of both compounds. The visual images of these particles taken with fluorescent microscopy were striking, and it was clear from the talk that this method is easily adapted to a wide range of organic compounds. On the basis of these early results, it seems very likely that ecologists will be hearing much more about this method in the near future.

The incorporation of mycorrhizas into the general science of ecology is part of a larger trend toward the melding of the ecology of macro- and microorganisms. This trend has been spurred on by researchers in many other fields (e.g. a symposium on this topic organized by Brendan Bohannan (University of Oregon, USA) at the 2006 ESA meeting) and is evidenced by special issues of *Ecology* that focused on microbes (88(6)) and tropical fungi (88(3)). This linkage of macro- and microecology is long overdue and is destined to expand in many new and unexpected ways. Mycorrhizal fungi have provided an important bridge between mycologists and ecologists, but they are just one example of the many pervasive interactions between plants and fungi and there is much room for expansion into pathogenic, commensalistic, and saprobic interactions as well.

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