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Perspectives on ICOM 6 "beyond the roots"

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From August 9 to 14, 2009, the Sixth International Conference on mycorrhizas brought together 290 participants from 41 countries to learn first-hand the latest information on mycorrhizal research. All activities and the housing for most participants were centered at the Ouro Minas Palace Hotel in the city of Belo Horizonte, Brazil. ICOM 6 was organized by the Microbiology Department of the Federal University of Viçosa and the International Mycorrhiza Society (IMS). The conference was organized around 11 topic areas covered in workshops, symposia, and poster sessions held on each of 4 days which gave time for informal debate and discussion outside formal sessions. One day midconference was devoted to tours to various scenic areas in the state of Minas Gerais. Topics were genome structure and evolution, cell biology and development, signal perception and metabolism, population structure, community diversity, plant–fungal community interactions, nutritional interactions, mycorrhizosphere interactions, stress tolerance, mycoheterotrophic interactions, and systematics of glomeromycetes. Of the presentations, 72 were oral and 218 were posters. Almost 72% of these concerned arbuscular mycorrhizal (AM) fungi, 25% involved ectomycorrhizal (ECM) fungi, and nearly 3% reported on coevolution, conservation potential, and diversity of fungi forming symbiosis with orchids. In this report, we can highlight the content of only a few of the excellent presentations and posters at ICOM 6, and we apologize to colleagues whose interesting work is not mentioned.

Jose Siqueira spoke at the opening ceremony and discussed the three decades of research on mycorrhizal symbioses conducted in Brazil. It was clear from his talk that the projects are as eclectic as the habitats spanning this large country. Even though some work done in the tropics was reported, considerable potential exists to accomplish much more in such an expansive natural laboratory.

A stimulating keynote lecture started each day. George Kowalchuk provided a broad overview of the application of genomics and metagenomics to elucidating community dynamics and processes occurring in soil microbes. All other keynote talks focused on AM fungi. Sally Smith provided insights into new ways of interpreting positive and negative consequences of phosphorus responses in mycorrhizal plants based on partitioning of P transfer pathways in the plant versus fungal symbiont. Paola Bonfante discussed recent developments in fungus–plant interactions at the cellular level, some of which were depicted in a breathtaking video. This and other reports provide striking evidence of the depth and breadth of AM fungus–plant coevolution. Lastly, Peter Young discussed progress on the *Glomus intraradices* genome project. While problems and challenges have plagued this project, valuable information is being obtained. Most notably, genome size is considerably larger than previously estimated, as is gene variability and organization. This species is a model organism, justified in part because of its ubiquity worldwide. The diversity of haplotypes, the ability to anastomose among populations, suggestions of putative recombination, and other interactions likely will not translate to other lineages, even within

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Glomus clades. Organization of the mtLSU gene, for example, was reported to be quite different in members of Gigasporaceae.

Benefits from completed genome sequence databases of several ECM fungal species were evident at this conference. Microarrays have been developed to measure gene expression; interference RNAs are being designed and expressed in transformants mediated by *Agrobacterium tumefaciens* T-DNA to selectively inhibit selective gene transcripts. Even in AM systems, microRNAs are being identified that have the potential to regulate and compare posttranscriptional activity of important genes.

Numerous studies were reported (39% of all presentations) analyzing diversity of AM and ECM fungi in a wide range of plant communities. Distinctions between population and community diversity remain blurred for both groups of fungal symbionts, as was evident not only from reports but also in conference topics and organization of reports in those topics. For AM fungi, physical evidence of sporulation continues to be a frequent source of data on species composition. However, gene sequences are providing an added dimension that not only help answer questions of intra- and interspecific variability but also provide insights into interpretations of morphology. While there still is a strong reliance on conserved rRNA genes for much of this work, other genes encoding beta-tubulin, ATPase subunits, and transcription factors are being tested. Several studies showed the critical importance of sample size, both in scale and amount. Speaking of scales, biogeographic patterns of ECM fungal distribution were elucidated from extensive herbarium specimens. A phylogeographic analysis just on the genus *Tuber* provided evidence of ECM fungi following postglacial migration of tree hosts. Biogeography of AM fungi focused less on distribution patterns and more on correlations of habitat and climatic variation with community structure.

The workshop on Glomeromycete systematics was contentious, which should come as no surprise. A proposal to erect three classes, two subclasses, and ten more orders using a limited set of morphological characters was not generally well received. A major concern is that selective use of characters from any data set to group and rank taxa without well-supported criteria will be misleading and cause more confusion than clarification. Despite the debates surrounding such changes, parsimony should reign supreme so that the classification can serve as a framework for testing hypotheses in other areas of research.

Use of public or commercial inocula received about the same attention as in previous ICOMs. Public acceptance, quality control, and scientifically meaningful field trials with suitable controls and baseline knowledge of indigenous fungal activity still are problematic issues. Cost–benefit analyses are sorely needed as well. As discussed in one report, major culture collections can play an important role in forging a link between basic and applied application of emerging technologies.

While the conference theme of "beyond the roots" drew attention to the broader ecological and social context of mycorrhizal symbiosis, it also stimulated attention to aspects of nutrition and symbiotic interface function. In her keynote lecture, Sally Smith presented an emerging body of evidence demonstrating that AM fungi can make a significant contribution to plant P uptake regardless of growth responsiveness of the host plant and that P uptake via the direct root pathway is often decreased in favor of the AM P uptake pathway. In nonresponsive plants, this AM contribution is "hidden" and can only be detected with radioactive P. These findings raise new questions across a range of scales; they have significant implications for crop breeding and may provide insights into a range of areas including understanding plant competition and heavy metal tolerance in AM plants and the evolutionary persistence of AM symbioses. The challenge now is to consider the import of this hidden nutrient uptake in each arena of research.

Significant developments in the identification and functional analysis of fungal transporters in mycorrhizal systems were addressed in several workshop presentations. The endosymbiosis between the glomeromycete *Geosiphon pyriformis* and the cyanobacteria *Nostoc punctiforme* was highlighted as a powerful tool for the identification and characterization of new fungal transporters. The use of functional yeast complementation was described to clone the first glomeromycete monosaccharide transporter. Uptake of hexoses by an AM fungus is a key step in nutrient exchange at the symbiotic interface, and identification and localization of orthologs in AM symbioses may be possible in the near future. In the model ECM species *Hebeloma cylindrosporum*, two high-affinity phosphate (Pi) transporters expressed in soil mycelium and ECM have been identified which mediate Pi/H^+ symport in yeast and share homology with AM fungal P transporters. Both transporters are differentially regulated by available P. Direct P uptake ability is reduced in non-ECM roots of ECM *Pinus pinaster*, which recalls the "switching off" of direct P uptake pathways and downregulation of root epidermal P transporters in AM symbioses. This work highlights the need to understand regulation of P uptake pathways in mycorrhizal symbioses.

The role of "C drain" as a cause of growth depressions was addressed in two complementary presentations that signal a shift in thinking in both ECM and AM research circles. The convention that mycorrhizal growth depressions result from reduced "cost-efficiency"—C supplied to roots or mycorrhiza per unit of nutrient gained—is being questioned and reassessed. Evidence was presented for a

symbiotic response in ECM as a function of nutrient status, in particular N, rather than C limitation. In addition, a reported absence of growth depressions in AM wheat plants when shaded (C-limited) and persistence of growth depressions even at low colonization (hence low C cost) points to a more subtle interplay that is yet to be deciphered. The question of whether C and P transfers are functionally linked in AM symbioses also was addressed. Studies of elemental concentration and distribution in an in vitro AM system showed that P accumulated in fungal hyphae when C allocation to roots was reduced. When the environment was modified to include root compartments of varied C supply, relatively little P was delivered to roots with a low C status. These data are indicative of a strong fungal control mechanism enabling selective P release to host tissues. The nature of this mechanism and the degree to which C and P transfer is mechanistically linked remain to be determined. It will be interesting to further corroborate these results in whole-plant systems.

Significant progress in the development and application of recently developed sophisticated methods for studying mycorrhiza formation and function was reported in several workshops. For example, using the SPring-8 synchrotron facility combined with resin embedded sections of mycorrhizal roots or hyphae prepared with freezing techniques was used to evaluate the role of AM fungi in cadmium (Cd) accumulation in the host plants. Cd was colocalized with polyphosphate fungal vacuoles in intraradical hyphae but not in plant cell walls. These results support previous conclusions that Cd originating from extraradical hyphal uptake is sequestrated in intraradical fungal structures and that contribution to the host Cd uptake is very low.

In vivo confocal imaging combined with in vitro mycorrhizal culture of transformed roots expressing specific GFP tags was used successfully to highlight important changes in root cells with development of the so-called prepenetration apparatus (PPA) in anticipation of AM fungal invasion. Cellular events occurring ahead of intracellular hyphal tips in these cells included reorganization of the nucleus, cytoskeleton, and endoplasmic reticulum; proliferation of Golgi stacks; accumulation of secretory vesicles, and synthesis of the perifungal membrane inside the PPA. The PPA thus can be envisaged as a complex cytoplasmic aggregation that concentrates all the cell machinery required for membrane proliferation at the site of fungal penetration and along the intracellular route of the hypha. First evidence also was presented that cell processes modified by symbiosis-related plant genes impact on root interactions by directly modulating AM fungal activity. When the expression of *G. intraradices* genes was followed during interactions with roots of wild-type *Medicago truncatula* or mycorrhiza-defective (Myc^-) mutants, all genes were expressed by spores germinating in wild-type root exudates or when appressoria were formed in association on wild-type roots. Inactivation of three *M. truncatula SYM* genes resulted in altered fungal gene expression (nonactivation or inhibition) and modified appressorium structure. Another original finding was a transcription factor from an AM fungus that can restore penetration of host tissues in a noninfective mutant of plant pathogen (*Colletotrichum lindemuthianum*). These results suggest similarity in control mechanisms of early morphogenetic events of host penetration by biotrophic fungi.

An in vitro sandwich culture system revealed that lateral root development in poplar is induced in the early phase of the ECM interaction with *Laccaria bicolor*. By oligo-array analysis of the root transcriptome, differential expression of nearly 3,000 genes was detected. Subsequent studies on differentially expressed genes involved in auxin transport and signaling pathways showed a rapid induction of a gene homolog of *Arabidopsis AtPIN2* involved in polar auxin transport and of several auxin signaling-related fungal genes during the early interaction phase. A model was proposed in which ECM fungus-induced auxin accumulation at the root apex stimulates lateral root formation through a mechanism involving auxin redistribution together with auxin signaling.

The local organizing committee chaired by Drs. Maria Kasuya and Mauricio Costa and former IMS President Larry Peterson and IMS board members all deserve our thanks and appreciation for making the conference memorable and stimulating. IMS will play an even more important role in ICOM 7, and so it is essential that anyone who wants to participate in the process become a member. ICOM 6 participants received membership with their registration, but attendance did not reflect the breadth of interested persons worldwide. The most important role of IMS is to provide an umbrella organization that fosters interactions and collaborations among its members. It helps that mycorrhizologists are an amazingly passionate and collegial group, as evidenced by song, dance, and general hilarity at both the Wines of the World and the dinner on the last night. We look forward to meeting again at the next ICOM, wherever that may be decided.