**Meetings**

**Mycorrhiza for all: an under-earth revolution**

7th International Conference on Mycorrhiza, in New Delhi, India, January 2013

In recent years, mycorrhizal research has undergone rapid expansion. Breakthroughs in genomics and other modern techniques have allowed us to break new ground in multiple domains, such as evolution, physiology, function, community patterns and biogeography of mycorrhizal fungi. The International Conference on Mycorrhiza (ICOM) is the most important platform for mycorrhizal scientists to present and discuss their work in both theoretical and applied areas of mycorrhizal symbiosis. ICOM 7 was held in New Delhi (India), January 6–11, 2013, and attracted over 400 participants from 48 countries. The theme of the conference was ‘Mycorrhiza for All: An Under-Earth Revolution’, stressing the importance of addressing scientific findings within an applied context to strengthen field implementations and improve sustainable agriculture (Fig. 1). It addressed the urgent need to apply mycorrhizal research to the environmental crises that threatens our planet.

**From genomic to functional analysis**

The last 10 yr have seen substantial increases in the genomic understanding of plants, including the pioneering full genomes of *Populus trichocarpa* and *Medicago truncatula* (Tuskan et al., 2006; Young et al., 2011). ICOM 7 highlighted parallel developments in the belowground partners in the mycorrhizal symbiosis. In particular, Francis Martin (INRA, France) accentuated the rapid expansion of complete genome decipherments for mycorrhizal fungi following the first genome sequences of *Laccaria bicolor* (Martin et al., 2008) and *Tuber melanosporum* (Martin et al., 2010). Identification of the genomic features that distinguish ectomycorrhizal (ECM) fungi from other mycorrhizal associations, such as ericoid and orchid mycorrhizas, and from parasitic or saprotrophic fungi will help to shed light on the evolution of the mycorrhizal symbiosis.

‘Reciprocal rewards stabilize the cooperation between plants and mycorrhizal fungi in order to avoid cheaters and less cooperative partners.’

These genomic data together with the recent transcriptomic analysis of *Glomus intraradices* (Tisserant et al., 2012), provide fundamental resources for physiological and functional research on symbiotic developmental and metabolic pathways. Natalia Requena (KIT, Germany) presented recent research on the mechanisms influencing plant–fungus recognition. She showed how *G. intraradices* secretes a protein, SP7, which counteracts plant immune program, consequently benefiting arbuscular mycorrhizal (AM) fungi colonization (Kloppholz et al., 2011). She also highlighted the role of the sugar transporter MST2 of *G. intraradices* in arbuscule formation (Helber et al., 2011). Similarly, Luisa Lanfranco (University of Turin, Italy) explored the molecular signals controlling the fungal morphogenesis via the analysis of *G. intraradices* NOX NADPH oxidase genes. Regarding the ECM symbiosis, Anders Tunlid (Lund University, Sweden) used spectroscopic analyses and transcriptome profiling to examine the mechanism by which the ECM fungus *Paxillus involutus* degrades organic matter when acquiring nitrogen (N) from plant litter. He observed that this fungus secretes similar enzymes to those involved in brown-rot fungi Fenton oxidative degradation (Rineau et al., 2012). Additionally, François Buscot (UFZ, Germany) investigated gene expression patterns linked to resources allocation processes in a multitrophic system form by oak roots, the ECM fungus *Piloderma croceum* and the root pathogen *Phytophthora quercina*. This emerging knowledge emphasizes the power of genomic data for understanding the establishment, durability and functionality of mycorrhizal symbioses.

![Fig. 1 ICOM 7 logo: ‘Mycorrhiza for All: An Under-Earth Revolution.’ It reflects the relevance of mycorrhizal research today. ‘The banyan tree is of extreme importance to the cultural heritage and legacy of India for ages. Its roots are mycorrhized by golden honey dew drops resembling mycorrhizal spores … prove to be the epicenter of a new revolution of which our planet is in dire need’ (ICOM 7 organizers; TERI, New Delhi, India).](image)
Nutrient trade terms

A central and re-occurring topic at ICOM 7 was the balance of reciprocal rewards (‘tit for tat’ principle) in mycorrhizal symbioses and the role of each partner in the establishment and transfer of nutrients across the soil–fungus–plant continuum. Recent research findings show that both-sided control of nutrient transfer exists between plant carbon (C) and fungal phosphorus (P; Lekberg et al., 2010; Hammer et al., 2011; Kiers et al., 2011) or N (Fellbaum et al., 2012), regulating the choice of partner and maintenance of evolutionary stability in AM symbiosis. In accordance with these results, Toby Kiers (Institute of Ecological Science, the Netherlands) presented this ‘fair trade’ system as a key evolutionary element. Reciprocal rewards stabilize the cooperation between plants and mycorhizal fungi in order to avoid cheaters and less cooperative partners. Opposing this general theory, Pierre-Emmanuel Courtay (University of Basel, Switzerland) indicated that there might be situations where investment and rewards are not directly correlated (Walder et al., 2012). Several presenters emphasized the additional complexity of reciprocal rewards in nutrient exchanges in natural communities connected by a common mycorrhizal network (CMN). Heike Bücking (South Dakota State University, Brookings, SD, USA) used shaded plants to manipulate the C strength, that is amount of C that is available to the plant for investments, while Edith Hammer (FU Berlin, Germany) used plants of different ages to measure nutrient allocation to CMN members investing different amounts of C into the mycelium network. Both conclude that C strength determines the plant’s access to nutrients in the CMN. However, Hammer and Marcel van der Heijden (Agroscope, Switzerland) pointed out that health status of the older plant, different species identity and adult-seeding species combinations can lead to outcomes differing from growth enhancement to strong repression of young plants. A situation where the ‘tit for tat’ principle is clearly undermined is in mycoheterotrophy. Duncan Cameron (University of Sheffield, UK) and Lee Taylor (University of Alaska, Fairbanks, AL, USA) both presented evidence that the parasitic C transfer to heterotrophic orchids occurs via N-compounds, most likely glutamine.

Regarding nutrient exchange in the mycorrhizal symbiosis, it has been assumed that sucrose is released into the mycorrhizal apoplasm and converted into glucose and fructose that are in turn assimilated by the fungus via transporters. However most of the molecular mechanisms involved in nutrient exchange are yet to be elucidated. Philipp Franken (IGZ, Germany) presented P- and C-transporter mutants that can help to clarify these gaps. Examining ectomycorrhizas, Uwe Nehls (University of Bremen, Germany) showed that a family of plant glucose facilitator genes (coding for SWEET proteins: Chen et al., 2010) is expressed during ECM formation. Consequently, it appears that this hexose could be the most important direct C source for the fungal partner in ECM. These findings support the concept that nutrients are main regulators of the mycorrhizal symbiosis in general, driving partner selection and the stability of the mutualism.

Population and community ecology

Identifying the drivers that structure mycorrhizal communities and populations was one of the hot topics during the conference. Many speakers highlighted the importance of biotic (host species) and abiotic (soil chemistry, rainfall, temperature) factors structuring mycorrhizal fungal communities. Nancy Johnson (North Arizona University, Flagstaff, AZ, USA) remarked that multiple-metrics experiments are necessary to characterize fungal communities. Further, Thorunn Helgason (University of York, UK) emphasized the need to consider temporal and environmental variation in designing sampling strategies for biogeography studies.

While several studies on fungal communities have rejected the Baas Becking hypothesis: ‘Everything is everywhere, but the environment selects’ (Taylor et al., 2006; Peay et al., 2007), Christina Hazard (University of Aberdeen, UK) presented results in an Ireland-based study suggesting that the Baas Becking hypothesis may be supported for AM fungi at a regional scale. From a broader scale, Leho Tedersoo (University of Tartu, Estonia) and Nadia Soudzilovskaia (VU-University of Amsterdam, the Netherlands) contributed to the mycorrhizal global distribution map (Read, 1991) forming novel hypotheses to explain mycorrhizal biogeography. From a community composition perspective, Tedersoo showed that host family strongly determines the phylogenetic structure of ECM fungi communities (Tedersoo et al., 2012). Taking a morphological approach, Soudzilovskaia showed that soil fertility and pH determined mycorrhizal infection. She observed that harsh environment relates with major mycorrhizal infection.

Most of the studies focused on either AM or ECM fungi, however, the mycorrhizal dominant type in an ecosystem is not a static feature but one that changes with time. To understand mycorrhizal type transitions it is necessary to understand their ecosystem functions. Ian Dickie (Landcare Research, Lincoln, New Zealand) tested several accepted opinions on functional differences between ECM and AM fungi and he concluded that some major concepts need to be re-examined, such as differences in mineral weathering, belowground feedback and foliar traits (Koele et al., 2012). Over a geological timescale, Jonathan Leake (University of Sheffield, UK) showed that from an evolutionary point of view the weathering function of mycorrhizas increases from AM to ECM and from gymnosperms to angiosperms, accelerating global biogeochemical cycles (Quirk et al., 2012). Both speakers highlighted the important role of mycorrhiza on geokochemical cycles as ecosystems drivers (Orwin et al., 2011).

The use of high-throughput sequencing techniques was a common methodology in many community studies. Novel techniques such as restriction-site DNA (RDA) and molecule real-time (SMRT) sequencing will contribute to more detailed information on AM fungal assemblages. The use of such techniques in AM studies continues adding information to the knowledge of AM fungal genetic diversity and therefore the Glomeromycota taxonomy is in a continuous state of change. One example was the suggestion of a major revision of Oehl et al. (2011) taxonomy proposed by Arthur Schüßler (University Munich, Germany). At the same time, the increased use of the MaarjAM database for...
AM fungi environmental studies brings an alternative to the traditional nomenclature using the virtual taxa (VT) nomenclature (Opik et al., 2010), that could help to solve the controversy in the Glomeromycota taxonomy.

Human use of mycorrhiza

Over-exploitation of natural resources and misuse of technological development have caused an environmental crisis with serious consequences for agronomic services (Tilman et al., 2002). ICOM 7 accentuated the applied aspects of mycorrhizal research. André Fortin (University of Laval, Quebec, Canada), Joyce M. Jefwa (CIAT, Nairobi, Kenya), and Alok Adholeya (TERI, New Delhi, India) presented progress in inoculum production and application that promote sustainable agriculture and rebuild soil biota. They highlighted the importance of isolating mycorrhizal strains with selected traits and functions, as well as the importance of producing inoculum compatible with conventional agricultural practices. Martina Janouskova (IEB, Prague, Czech Republic) emphasized the necessity to investigate the competitive performance and persistence of the inoculum, when applied to natural soils, with the existing AMF community. Presenters described current research programs that apply different types of mycorrhizal fungi; such as ECM fungi for forests conservation, AM fungi to tropical reforestation and Sebacinales fungi, which also form orchid mycorrhiza, to increase switchgrass production. Another potential application presented by Mohamed Hijri (University of Montreal, Canada) was the use of AM inoculum as biological control organisms for pathogens. Speakers also highlighted the importance of considering the impact of agricultural practices on the native mycorrhizal community to achieve successful land management practices. In this context, Luise Olbrecht (Agroscope, Switzerland) showed that soil tillage drastically changes AM fungal communities with direct consequences on plant communities and nutrient leaching losses. Many speakers addressed environmental applications, looking at the effects of mycorrhizal fungi on plant growth under harsh conditions, and their utility in phytoremediation of polluted soils. Contributing to this research field, John Klironomos (University of Guelph, Canada) stressed that one of the major benefits of mycorrhizal symbiosis to plants is the increase of host niche size and therefore mycorrhizal fungi might favor plants growing under stressful conditions and in variable environments. Applied knowledge of mycorrhizas is of worldwide interest because it addresses the current urgency to develop methods that guarantee world food supply and ecosystems conservation.

Future directions

Mycorrhizal science is progressing quickly. When we look back at previous ICOMs, we observed that ICOM 5 (2006, Granada) represented a turning point, as Selosse & Duplessis (2006) highlighted in ICOM 5 report section titled “The dawn of genomics in the mycorrhizal world”. It is encouraging to see how genomics has helped to clarify previous gaps, such as molecular mechanisms on the plant–fungus interface, evolution or biogeography.

Two of the emerging research areas from ICOM 7 were the functioning of mycorrhizas in biogeochemical cycles (cf. Nøs宏伟l et al., 2013) and the complexity of multitrophic interactions in the rhizosphere. Addressing these questions requires an integration of disciplines such as chemistry, geology and pedobiology with more traditional mycorrhizal disciplines such as ecology, physiology and mycology. We believe that the theme of the next ICOM (ICOM 8) ‘Mycorrhizal Integration across Continents and Scales’, to be held in Flagstaff (Arizona, USA), August 26–31, 2015, will provide a perfect framework for discussions towards this end.

Acknowledgements

The authors acknowledge the Energy and Resources Institute (TERI) and the International Mycorrhiza Society for organizing the conference. They also thank all the attendees who contributed with talks and posters and provided a stimulating forum including, and especially those whose names are not mentioned here due to space constrains. The authors thank F. Martin, I. Dickie and S. Hortal for helpful comments on the report. L.B.M-G. acknowledges core funding for Crown Research Institutes from the New Zealand Ministry of Business, Innovation and Employment’s Science and Innovation Group through the Landcare Research Hayward Post-doctoral Fellowship. E.C.H. acknowledges the Marie Curie post-doctoral fellowship NANOSOIL, and K.G., the French Minister of Research and Technology. A.V.’s laboratory is supported by the Laboratory of Excellence ARBRE (ANR-12-LABXARBRE-01).

Laura B. Martinez-Garcia1*, Kevin Garcia2, Edith C. Hammer3 and Alice Vaysseies4

1Ecosystems and Global Change, Landcare Research, PO Box 40, Lincoln, 7608, New Zealand;
2Unité de Biochimie et Physiologie Moléculaire des Plantes, SupAgro, IBIP – Bât. 7 – 2 place Pierre Viala, 34060, Montpellier, France;
3Plant Ecology, Freie Universität Berlin, Altensteinstr. 6, 14195, Berlin, Germany;
4Interactions Arbres/Micro-organismes, UMR 1136 INRA, Université de Lorraine, Institut National de la Recherche Agronomique, Centre INRA de Nancy, 54280, Champenoux, France

(*Author for correspondence: tel +64 3 321 9999; email laurabeatrizmartinez@gmail.com)

References
