# Meetings

## Mycorrhizas: dynamic and complex networks of power and influence

### 33rd New Phytologist Symposium – Networks of Power and Influence: ecology and evolution of symbioses between plants and mycorrhizal fungi, Zürich, Switzerland, May 2014

Plants and mycorrhizal fungi form complex symbiotic relationships belowground that can result in beneficial or disadvantageous outcomes for one or both of the symbiotic partners. It is one of the most ancient and widespread symbioses on earth (Smith & Read, 2008). Since the research field on mycorrhizas developed in the middle of the last century, the scientific community has generated an enormous amount of knowledge on the ecology, evolution and striking importance of mycorrhizas for ecosystems worldwide. However, many key questions still remain unresolved, that new tools in genomics, isotopic analyses, and statistical approaches are only now making tractable.

The 33rd New Phytologist Symposium on 'Networks of Power and Influence: ecology and evolution of symbioses between plants and mycorrhizal fungi', a title inspired by a paper of Leake *et al.* (2004), was held in Zürich, Switzerland. The meeting provided one of the rare opportunities where the global community of mycorrhizal researchers could get together to present the latest advances in the field and discuss striking questions like: How did the mycorrhizal symbiosis evolve? Which conditions determine whether the symbiosis turns out to be mutualistic or parasitic? What is the mycorrhizal contribution to the sustainability of ecosystems and can mycorrhizal fungi be used for sustainable plant production? How can we increase the awareness of the mycorrhizal importance for ecosystem functioning worldwide?

*'. . . To fully understand the nature of the symbiosis, it is essential to consider all of the temporal, spatial, and environmental conditions symbiotic partners may experience . . .'*

There was huge interest in the meeting with over 100 people on the waiting list, extensive and high level discussions, and high quality presentations including > 100 posters. Here we highlight four of the most exciting topics that were discussed during the meeting.

### Providers, cheaters or insurers? – mycorrhizal phenotypes

While the mycorrhizal symbiosis is usually considered a mutualistic relationship, many examples exist where plants are apparently not benefitting from the mycorrhizal association. The same may hold true for the fungal partners, although this is far less well studied, in particular due to the obligate nature of the association for the majority of mycorrhizal fungi. This variation in responses of the symbiotic partners was described by the term 'mutualism–parasitism continuum' (Johnson *et al.*, 1997). During the meeting, several examples were shown of how the mycorrhizal symbiosis, not only directly but also indirectly, affects plant performance by modifying the wider biotic and abiotic environment. Mycorrhizal effects on herbivore–plant interactions (Babikova *et al.*, 2013), soil structure (Rillig & Mummey, 2006), other plant symbionts (Larimer *et al.*, 2014), or multiple ecosystem functions (Wagg *et al.*, 2014) can indirectly affect plant performance and provide benefits for the plants that are not easy to identify. Also plant fitness, that is, the effects of the symbiosis on the three components of individual plant performance (growth, reproduction and survival) is rarely addressed.

Beyond the multi-dimensionality of potential benefits, the spatio-temporal variation along the continuum is also important. Symbioses can be beneficial 'here and now' but can reduce the symbionts' fitness in another environmental context (e.g. stress conditions) or ontogenic stage (e.g. immature seedlings vs reproductive individuals). For example, John Klironomos (University of British Columbia, Canada) presented data which suggested that mycorrhizal fungi may provide benefits to the plants under extreme environmental conditions, while under optimal conditions the symbiosis may represent a net cost for the plant. Therefore, the mycorrhizal symbiosis could be regarded as an insurance policy for the plant.

It becomes increasingly clear that the mycorrhizal symbiosis is much more complex than a simple nutrient-for-carbon trading business. The use of the term parasitism might give an unbalanced view of the far-reaching complexity of plant–fungal relationships. It was therefore proposed by Sally Smith (University of Adelaide, Australia) to move away from the mutualism–parasitism continuum, and instead speak of a 'responsiveness continuum'. To fully understand the nature of the symbiosis, it is essential to consider all of the temporal, spatial, and environmental conditions symbiotic partners may experience during one, or even more lifespans.

## Facing complexity with curiosity: importing concepts and methods from other disciplines

Another key aspect arising from the Symposium was the complexity of mycorrhizal associations from a physiological, ecological, or evolutionary point of view. To face this complexity, researchers are importing concepts and methods from other areas of research. Toby Kiers (Vrije Universiteit Amsterdam, the Netherlands) presented how economic market theory can be adapted to explain the evolution and stability of cooperation in the mycorrhizal system. The paradox of cooperation between both partners of the mycorrhizal symbiosis can be partially explained by the ability of the host to dedicate more carbon to their best partners (Kiers *et al.*, 2011) and of the symbiont to differentially allocate nutrients to individual plant hosts (depending on the amount of carbon they provide) in a common mycorrhizal network (Fellbaum *et al.*, 2014). This ability to impact the fitness of the partner, with regard to the benefits it provides in terms of nutrient exchange, seems to play a key role in the stabilization of mycorrhizal interactions. Another example on how the symbionts can control the fitness of their partners was presented by Francis Martin (INRA Nancy, France) showing how fungal effector proteins can control plant immunity (Plett *et al.*, 2014). These results stimulated the discussion whether the logo of the Symposium, showing fungi and plants shaking hands, should rather be modified to both wearing boxing gloves or even carrying knives (Fig. 1).

Mathematics and computer science can also provide a source of new ideas, as argued by Alicia Montesinos-Navarro (Universidad Nacional Autonóma de México, Mexico). She introduced ecological network theory to reveal the underlying processes of how multi-specific interactions between arbuscular mycorrhizal fungi and plants influence plant community structure. This network shows a high modularity, which is new evidence of selectivity in mycorrhizal interactions at the community level. Network theory was also mentioned by Ian Dickie (Lincoln University, New Zealand) and colleagues as a relevant tool to understand the driving forces behind mycorrhizal community structure through ecosystem development. Using a 120 000 yr chronosequence of temperate rainforest ecosystem development dominated by arbuscular mycorrhizal plants, they found no change in network nestedness along the succession. Interestingly, the network position (degree of centrality) of partners partially predicted new links during the ecosystem development.

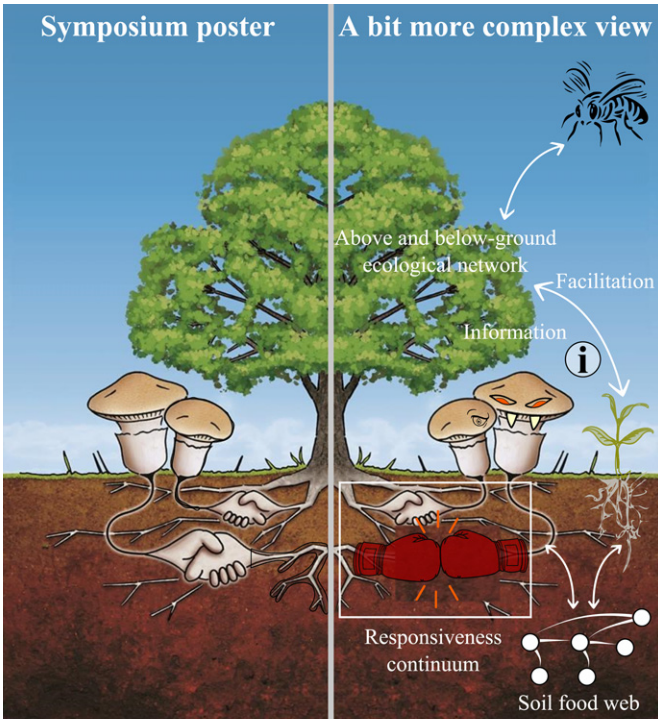


**Fig. 1** The original conference poster (left) and a slight modification paying respect to the complexity of mycorrhizal associations and their environment (right).

Finally, there is a general call for the use of functional traits in mycorrhizal research, as the current categorical frameworks (e.g. saprotroph, pathogen, endophyte), are unsatisfactory to infer ecological strategies and to categorize fungi because several categories may apply to the same organism. Indeed, functional ecology allows for going beyond a taxonomic view of biodiversity and was proven to be very informative at the community and ecosystem scale. The call for using functional traits is not new (see van der Heijden & Scheublin, 2007; Parrent *et al.*, 2010), but recent technological advances (e.g. enzymatic activity profiling, isotopic tracing, etc.) may pave the way for incorporating functional ecology in modern mycorrhizal science, as argued by Carlos Aguilar-Trigueros (Freie Universität Berlin, Germany).

## Mycorrhizal genomics, evolution and food security

The repeated emergence of mycoheterotrophy in plant evolution potentially challenges the sustainability of mycorrhizal networks, as discussed by Marc-André Selosse (Muséum national d'Histoire naturelle, Paris, France). By taking advantage of these networks, these plants without any photosynthetic capability are able to receive carbon from neighboring plants and survive in a low-light environment. Examples of fully mycoheterotrophic plants from Ericaceae and Orchidaceae were shown together with examples of plants in intermediate evolutionary steps with a mixotrophic metabolism, but interestingly the dependency of mixotrophic species on photosynthesis for seed production may limit their evolution to full mycoheterotrophy (Gonneau *et al.*, 2014). The ability of orchids to acquire carbon from mycorrhizal fungi is indeed a key process in their metabolism and recent transcriptomic and proteomic data are finally shedding some light on the molecular mechanisms underlying orchid mycorrhizal symbiosis (Perotto *et al.*, 2014; Valadares *et al.*, 2014).

The results emerging from the '-omic' sciences were the basis for discussion in the last session of the meeting. Francis Martin and David Hibbett (Clark University, Worcester, MA, USA) showed the progress of the Mycorrhizal Genomics Initiative, which has already publicly released the draft genome for 31 mycorrhizal fungi. Comparative analyses of ectomycorrhizal genomes suggested parallels between the evolution of ectomycorrhizas and 'brown rot' wood decay. However, ectomycorrhizal species are polyphyletic in origin, and while converging on a symbiotic lifestyle, each ectomycorrhizal clade has retained a unique array of decay-related enzymes, suggesting that they possess diverse decomposing capabilities. Also noteworthy was the genome analysis of ectomycorrhizal root tips (Plett & Martin, 2011). This analysis indicates that convergent ectomycorrhizal evolution is probably related to the deployment of a 'symbiosis genetic toolkit', which includes the loss of plant cell wall degradation enzymes and the gain of mycorrhiza-induced small secreted effector-like proteins such as MiSSP7 that control plant development and immunity (Plett *et al.*, 2014).

Ian Sanders (University of Lausanne, Switzerland), promoted exciting discussions by coupling evolutionary genomics of mycorrhizal fungi with field experiments. During his talk, he demonstrated how genetic variation in *Rhizophagus irregularis* (also addressed on the poster by Tania Wyss (University of Lausanne, Switzerland) who was awarded the Symposium poster prize) can be used to increase yields of cassava in real-world agricultural settings, demonstrating the importance of mycorrhizal fungi for food security in developing countries.

## Respect mycorrhizas! Raising the awareness in other disciplines

By providing a platform for researchers working on soil biodiversity and plant–soil interactions in general, the Symposium paid respect to the fact that mycorrhizas should not be considered away from their wider biotic environment. Wim van der Putten (Netherlands Institute of Ecology, Wageningen, the Netherlands) presented the concept of 'plant–soil feedback' as a useful approach to explain the structure of ecosystems, and addressed the importance of disentangling the underlying network interactions among soil biota to enable the track down of causal effects. Bernhard Schmid (University of Zürich, Switzerland) presented new insights into how plant biodiversity effects can be influenced by soil biota, suggesting that the co-evolution of plant–soil communities is an intrinsic feature of ecosystems.

However, it also turned out that there is a discrepancy between the mycorrhizal research community and other disciplines in the recognition of the mycorrhizal symbiosis. While mycorrhizal researchers widely accept the fundamental role played by mycorrhizal fungi in terrestrial ecosystems, these organisms still attract little attention in current soil food-web theory (see e.g. Neutel *et al.*, 2007). It was discussed that this might be attributed to the fact that many of the data on mycorrhizal contributions to ecosystem performance have been generated from model systems under glasshouse conditions, often using sterilized soils and artificial plant–soil–fungus combinations. It was suggested by Wim van der Putten that we should plan experiments based on 'what you find in nature'. By conducting glasshouse experiments using combinations that can be found in real situations, ecological realism could be enhanced, and the undoubted important role mycorrhizal fungi play worldwide would receive further recognition.

## Conclusions

The emergence of new approaches and technologies applied to the mycorrhizal symbiosis is constantly increasing our knowledge about plant–fungal interactions. However, as we learn more, new and amazing questions are raised. Overall, it is necessary to strengthen the dialogue among disciplines in order to capture the complexity of mycorrhizal interactions. Meetings like the 33rd New Phytologist Symposium are crucial to achieve this objective.

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