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IMS Newsletter

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The International Mycorrhiza Society quarterly e-newsletter



'Symbiosis'
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CONTENT:

Editorial	2
Top 10 papers	6
ICOM11 highlights	7
ESA highlights	15
Research commentaries	19
YouTube interviews	25
Tools	26
Events & announcements	27
IMS Executive	29

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Editorial: ICOM11 highlights and awards, new IMS Board, and more

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Every two years the worldwide mycorrhizal community joins to present the most recent advances on mycorrhizal research. This year, the 11th International Conference on Mycorrhiza (ICOM11) and the 5th International Molecular Mycorrhiza Meeting (iMMM5) took place online (1 – 4 August 2022) due to the restrictions of the COVID-19 pandemic. It was organized by the International Mycorrhiza Society (IMS), the Mycological Society of China, the Chinese Society for Plant Biology, the Institute of Microbiology of the Chinese Academy of Science, and the CAS Center for Excellence in Molecular Plant Science, with Prof. Liangdong Guo and Prof. Ertao Wang as chairs.

The mycorrhizal research field is very broad and interdisciplinary including a wide range of research fields such as ecology, evolution, agronomy, molecular biology, forestry, molecular cross-talk and trade, to edible mushrooms, mycorrhizas & pollution, mycorrhizas & restoration, among others. The full program of this years ICOM11 is available at: <https://icom11.casconf.cn/>). In addition to wonderful keynote talks, Francis Martin and Marcel G.A. van der Heijden summarized the current state of the art and provided an outlook on research developments in the mycorrhizal research field focusing on

environmental genomics, ecology & agriculture. Francis Martin showed that the comparison of whole genomes of hundreds and hundreds of genomes from fungi with different ecological roles (mycorrhizas, wood decayers, and soil decomposers), revealed several independent transitions from saprotrophism to symbiosis in the fungal Kingdom. Hundreds of symbiosis-related genes have been identified through metatranscriptomics; the analyses of the expression of such genes can help us to understand the role of saprotrophic and mycorrhizal fungi in terrestrial carbon and nitrogen cycling. Marcel G.A. van der Heijden argued that while mycorrhizal fungi have been shown to have a great impact on plant productivity of natural ecosystems, their effects on agricultural systems is less clear. It is not clear yet under which conditions mycorrhizal bioinoculants are having positive effects on crops – several recent studies and meta-analysis show that effects are highly variable and many commercial inoculants do not contain viable propagules. Several highlights of ICOM11 are summarized on page 7-19, including those focusing on ecology (by Justine Karst, page 7), applications (Pedro M. Antunes, page 9), and molecular biology (Johanna Wong-Bajracharya and Jonathan M Plett, page 12).

IMS awards and updated Board of Directors
Four awards were given during ICOM11:

- Student Award for Excellence in Mycorrhiza Research Publication: Johanna Wong-Bajracharya, from the Department of Primary Industries New South Wales, Australia, for her *PNAS* article entitled “The ectomycorrhizal fungus *Pisolithus microcarpus* encodes a microRNA involved in cross-kingdom gene silencing during symbiosis”, which shows how *P. microcarpus* encodes a microRNA entering plant cells and stabilizing the symbiosis. This article was the No. 1 paper of the last 3 months in our last issue (Issue 3, Vol. 2) Top 10 vote. Check a YouTube interview to Johanna in page 25.

- Early Career for Excellence in Mycorrhiza Research Publication: Vasilis Kokkoris, from the Department of Ecological Science, Vrije Universiteit Amsterdam, Netherlands, for his *Curr Biol* paper entitled “Host identity influences nuclear dynamics in arbuscular mycorrhizal fungi”.

- Mid-Career Mycorrhiza Research Excellence Award: Maarja Öpik, Director of the Institute of Ecology and Earth Sciences, University of Tartu, Estonia, for her work focusing on the molecular detection and identification of arbuscular mycorrhizal fungi.

- Eminent Mycorrhiza Researcher Award: Jim Bever, from the Department of Ecology and Evolutionary Biology, University of Kansas, United States, for his contribution to the mycorrhizal research field, especially his work on plant-soil feedbacks, and the role of mycorrhizas in ecosystems and in prairie restoration.

- Eminent Mycorrhiza Researcher Award: Francis Martin, from the National Research Institute for Agriculture, Food and Environment (INRAE), France, for his contributions to the mycorrhizal research field, especially ground breaking studies linked to the genomics and large scale sequencing efforts of mycorrhizal fungi.



Johanna Wong-Bajracharya



Vasilis Kokkoris



Maarja Öpik



Jim Bever

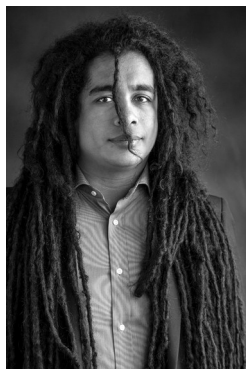


Francis Martin

In addition, we have elected new members of the IMS Board of Directors: Justine Karst (University of Alberta) was elected as the vice-president and will become president in two years. We also welcome three new Board members: César Marín (Santo Tomás University, Chile) as IMS Newsletter Editor-in-Chief, Patricia-Silva-Flores (Pontifical Catholic University of Maule; check page 28 for further information) as Director of Communications, and David Johnson (University of Manchester) as ICOM12 organizer. Please find the full list of Directors in page 29. We would like to thank all further candidates for their interest and willingness to serve the IMS and hope they have interest to be nominated again further in future. In addition, the terms of Prof. Miranda Hart (University of British Columbia – Okanagan) and Prof. Liang-Dong Guo (Beijing Institute of Microbiology and Epidemiology) within the board of directors were ending. We would like to thank them for their excellent contribution to the IMS and the mycorrhizal research field in general.



Justine Karst



César Marín



Patricia Silva-Flores



David Johnson

In this issue...

The Top 10 mycorrhizal research papers of the last four months (papers published between May and August, 2022), include in ranking 1 a *Trends Ecol Evol* review by Bala Chaudhary and co-authors about different definitions for mycorrhizal traits, including plant, fungal, and symbiotic mycorrhizal traits. The ranking 2 was a *Mycorrhiza* review by Stephanie J. Watts-Williams on the use of stable or radioactive isotope labelling to elucidate the mycorrhizal uptake pathways. The ranking 3 was also a review, published in *Annu Rev Plant Biol* by Alison E. Bennett and Karin Groten about the costs and benefits of interactions between plants and arbuscular mycorrhizal fungi (AMF).

Besides ICOM11 highlights, please find on page 15, mycorrhizal ecology highlights (by Justine Karst and co-authors) of the Ecological Society of America – Canadian Society for Ecology Evolution Joint Meeting, 2022, which included over 100 presentations focused on mycorrhizas. As usual, this issue includes two research commentaries: one by Carlos Urcelay and co-authors about the need to distinguish between response and effect traits in AMF, and about a recent meta-analysis of his group published in *New Phytol* about the different effects of AMF genera on plant and soil ecosystem functions. A second research commentary by María Isabel Mujica and Marc-André Selosse describes the waiting room hypothesis, which postulates that mycorrhizal habit might have evolved from root endophytism in Orchidaceae, showing several cases which give empirical support to this hypothesis. Please stay tuned (in the following issues) for further written interviews with leading mycorrhizal researchers from around the world, about their lives, research, and advice, among others.

Finally, in addition to our usual Tools and

Events sections, find YouTube interviews with Jonathan Plett on effector proteins in fungi, and to his former student and IMS student award winner, Johanna Wong-Bajracharya on how ectomycorrhizal fungi may regulate host gene expression through microRNAs.



Top 10 papers on mycorrhizal research*

1. Chaudhary VB, Holland EP, Charman-Anderson S, *et al.* 2022. What are mycorrhizal traits? *Trends Ecol Evol* 37:573-581. <https://doi.org/10.1016/j.tree.2022.04.003>
2. Watts-Williams SJ. 2022. Track and trace: how soil labelling techniques have revealed the secrets of resource transport in the arbuscular mycorrhizal symbiosis. *Mycorrhiza* 32:257-267. <https://doi.org/10.1007/s00572-022-01080-7>
3. Bennett AE, Groten K. 2022. The costs and benefits of plant–arbuscular mycorrhizal fungal interactions. *Annu Rev Plant Biol* 73:649-672. <https://doi.org/10.1146/annurev-arplant-102820-124504>
4. Law SR, Serrano AR, Daguerre Y, *et al.* 2022. Metatranscriptomics captures dynamic shifts in mycorrhizal coordination in boreal forests. *Proc Natl Acad Sci USA* 119:e2118852119. <https://doi.org/10.1073/pnas.2118852119>
5. Suetsugu K, Haraguchi TF, Tayasu I. 2022. Novel mycorrhizal cheating in a green orchid: *Cremastra appendiculata* depends on carbon from deadwood through fungal associations. *New Phytol* 235:333-343. <https://doi.org/10.1111/nph.17313>
6. Fu W, Chen B, Rillig MC, *et al.* 2022. Community response of arbuscular mycorrhizal fungi to extreme drought in a cold-temperate grassland. *New Phytol* 234:2003-2017. <https://doi.org/10.1111/nph.17692>
7. Fei S, Kivlin SN, Domke GM, *et al.* 2022. Coupling of plant and mycorrhizal fungal diversity: its occurrence, relevance, and possible implications under global change. *New Phytol* 234:1960-1966. <https://doi.org/10.1111/nph.17954>
8. Zhu X, Zhang Z, Wang Q, *et al.* 2022. More soil organic carbon is sequestered through the mycelium-pathway than through the root-pathway under nitrogen enrichment in an alpine forest. *Glob Chang Biol* 28:4947-4961. <https://doi.org/10.1111/gcb.16263>
9. Högberg P, Högberg MN. 2022. Does successful forest regeneration require the nursing of seedlings by nurse trees through mycorrhizal interconnections? *For Ecol Manag* 516:120252. <https://doi.org/10.1016/j.foreco.2022.120252>
10. Jevon FV, Lang AK. 2022. Tree biomass allocation differs by mycorrhizal association. *Ecology* 103:e3688. <https://doi.org/10.1002/ecy.3688>

*Selected from 132 Web of Science articles published between *May – August*, 2022 by: Justine Karst, Jonathan Plett, Melanie Jones, Marcel van der Heijden, Francis Martin, Jan Jansa, John Klironomos, Liang-Dong Guo, Miranda Hart, Jason Hoeksema, Judith Lundberg-Felten, Bala Chaudhary, Annegret Kohler, Joseph Cooper, Junling Zhang, and César Marín.

ICOM11 highlights

ECOLOGY

Justine Karst¹

¹University of Alberta, Canada.

Ecology was sprinkled throughout the scientific program at ICOM11, whether it was understanding big-scale biogeography or small-scale molecular mechanisms. While I would certainly like to share details on all the talks and posters, I will just highlight a few themes and presentations that I was particularly inspired by.

How mycorrhizas respond to global change has directed the research of many mycorrhizal scientists. This year, we saw presentations that covered various aspects of global change including: species invasions, climate change (e.g. drought, heat, fire), and nitrogen deposition. The long-term research conducted by Kitty Gehring and her team on pinyon pines in southwest United States has informed mycorrhizal ecology in many ways, and it continues to do so as an early look on the effects of climate change in woodlands. Her work highlights that it is the combination of stressors—in this case, drought and heat—that mostly decrease the abundance and diversity of ectomycorrhizal (EM) fungi. In addition to drought, fires have also increased in frequency and intensity in this region, which have promoted invasion by cheatgrass. Surprisingly, between fire and plant invasion, plant invasion had the greatest effect on reducing EM colonization of pinyon pine. As part of mitigating these stressors, the Gehring lab has investigated approaches to restore cottonwoods, a riparian tree species known for creating ribbons of green in the southwest United States. Encouragingly, they have found that cottonwood survival can be

improved by up to 80% depending on mycorrhizal inoculum type.

Owing to its threatened status and tremendous role in carbon sequestration, grasslands are critical ecosystems in which to examine the roles played by mycorrhizas. There were several interesting talks of various studies situated in Chinese grasslands. Wei Fu & Baodong Chen demonstrated that intense drought reduced the richness of arbuscular mycorrhizal fungi (AMF) more than chronic drought applied over three years. In turn, the community response of AMF was influenced by the plant community diversity and productivity. Interestingly, the relative allocation of plants to belowground biomass mediated the response of AMF diversity to drought. Gaowen Yang et al. extended our understanding on AMF in grassland plant ecology with their review on the relationship between AMF and ecosystem stability. By looking across several recent studies, they showed that AMF increase temporal stability of plant community productivity by increasing plant species asynchrony and by temporally stabilizing plant nutrient uptake. By combining results across these studies, they then developed a framework for understanding the direct and indirect links between soil microbes and plant communities.

Of course, we all know the important role mycorrhizal fungi play in controlling large scale carbon and nutrient cycles, which is particularly relevant to climate change. I loved the cross-scale approach used by Stephanie Kivlin *et al.* to understand the niches of fungal symbionts at global and local scales, and predict the response of soil fungi to climate change. Global species distribution models

for over 400 individual fungal taxa revealed the importance of climate, i.e., potential evapotranspiration and mean annual temperature, on determining where these fungi are found worldwide. Based on the importance of climate in determining species' niches, they then surveyed fungi along an elevational gradient as a space-for-time substitution of climate change, but found no effect of climate on the community composition of AMF. Instead, they found that host-specificity structured AM fungal community composition. These results suggest that models predicting fungal species' distributions at the global scale fall short of predicting species composition at the local scale, and additional variables, such as plant species distributions will be needed to close the gap. Finally, Kivlin *et al.* gave us a peak at data showing that 29 years of warming had less effects on the community composition of soil fungi than shifts in the timing of snowmelt, which had only been experimentally manipulated for four years.

Not only has the research community investigated the response of mycorrhizas to climate change, we are now making progress in understanding how mycorrhizas may help mitigate climate change. Colin Averill *et al.* presented results from >100 long term forest monitoring plots distributed across continental Europe to show that 3-fold variation in tree growth and carbon capture is linked to changes in ectomycorrhizal fungal community composition. In addition to these published findings, he also presented early results from a large-scale forest restoration experiment where tree seedlings receiving tailored soil inoculum are outperforming those receiving none. Though still preliminary, Averill suggested that their research points to a way to drawdown carbon from the atmosphere by harnessing mycorrhizal fungi that increase tree growth.

However, as Marcel van der Heijden pointed out in his Perspectives & Outlook on Mycorrhizal Research, it will be important to investigate under which ecological conditions mycorrhizal inoculum is needed and why. It is unlikely that adding soil inoculum will be a singular solution across all disturbances to improve tree performance.

For years, mycorrhizas were studied for their influence on plant nutrition, growth, and establishment. Over the past decade, we have seen a pronounced shift to studying the influence of mycorrhizal fungi on ecosystem processes, notably carbon and nutrient cycling. Nowhere is this shift in thinking most evident than in research on the influence of tree mycorrhizal type on stand biogeochemistry. However, the dichotomy between ectomycorrhizal and arbuscular mycorrhizal effects on ecosystem processes has become more nuanced, such that there is more focus on how the community composition within a mycorrhizal type influences nutrient cycling. For instance, Camille Truong *et al.*, and Sarah Sapsford & Ian Dickie demonstrated that changes in community composition of ectomycorrhizal fungi shape nitrogen availability and soil enzymatic functions, respectively.

Although we arrive at ICOM to learn about mycorrhizas, we, of course, appreciate that mycorrhizal fungi do not function alone! We know that 'mycorrhizal-helper-bacteria' are important in fungal acquisition of resources, but Jan Jansa and his team added a new twist; protists that consume bacteria release nitrogen that is then used by AMF and its plant partner. Furthermore, Ningkang *et al.* demonstrated that using chemotaxis, bacteria swim towards AM fungal hyphae, and hyphae are the highways that bacteria use to transport themselves to organic phosphorus patches. These are fascinating

examples of the inter-kingdom interactions that make up the mycorrhizal hyphosphere.

Finally, I, along with Melanie Jones and Jason Hoeksema, evaluated claims in the popular media about the structure and function of common mycorrhizal networks in forests. The 1997 study by Simard *et al.*, which Melanie was a part of, was groundbreaking because it was the first replicated, controlled field study on ectomycorrhizal common mycorrhizal networks. The 'wood-wide web' has since captured the interest of broad audiences. We are concerned, however, that claims in the popular media are disconnected from evidence, and that bias toward citing positive effects of common mycorrhizal networks, has developed in the scientific literature. The proximate reasons for taking on this challenge varied; Melanie was bothered by sloppy citing of mycorrhizal network studies, Justine became concerned when her son said that he learned at school that trees talk to one another through fungal networks, and Jason was triggered by an episode of *Ted Lasso*. The ultimate reason for addressing this issue, however, was the same for all of us: to protect the integrity of science. Stay tuned for more developments!

APPLICATIONS

Pedro M. Antunes²

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I will highlight contributions directly focused on mycorrhizal applications, especially those capable of driving innovations that promote ecosystem resistance and resilience, mitigate global change factors, help restore compromised systems, and contribute to a more sustainable agriculture.

Commercial inoculants stand out as a staple of mycorrhizal applications. However, M.J. Salomon showed that 80% of the many AMF

commercial inoculants they tested under laboratory conditions failed to establish and field testing was also inconsistent. Consistently, Marcel van der Heijden revealed that the effectiveness of AMF inoculation across >50 maize fields in Switzerland increased productivity up to 40%, but only in a quarter of the fields. In addition, root colonization was not a predictor of yield responses. Clearly, the use of currently available, non-native commercial mycorrhizal inoculants containing haphazardly selected fungal isolates is problematic, as it was also highlighted by Miranda Hart. Conceivably, recent advances in AMF genetics may result in a directional shift towards catered inoculants for which we have a better understanding of genetic traits. On this point, Nicolas Corradi showed how his team is investigating the role of AMF genomics in host responses through single nucleus analysis, and Francis Martin provided an account of how meta-transcriptomics and genome comparisons among fungi with different lifestyles are contributing to identify genes associated with key symbiotic responses. Meanwhile, several studies highlighted the relevance of indigenous mycorrhizal communities under various 'applications' contexts. For example, ecosystem restoration is a key area in relation to mycorrhiza management. Compromised sites are typically restored to support a specific reference plant community and plant seedlings are produced towards that goal. However, Nicole Hynson *et al.* reminded us that mycorrhizal and plant communities may be co-dependent. Using next generation sequencing (NGS) metabarcoding to compare AMF community composition in forest sites in Hawaii where restoration stalled against remnant intact sites uncovered discrepancies, suggesting that ecosystem restoration practices should also be guided by using indigenous mycorrhizal communities as reference points. Liz Koziol & James Bever

presented data from prairie restoration studies showing that indigenous AMF are consistently better promoters of plant establishment and growth than AMF commercial inoculants. They did point out the major challenge of developing methodologies to produce and distribute these indigenous inoculants (an issue also addressed by Hu Wentao *et al.*) but their work either testing different densities of indigenous AMF inoculum across a density gradient or inoculating plots using nurse plants clearly indicated that using indigenous AMF in restoration is preferable. In another study, James Bever *et al.* revealed that specific AMF species can drive positive feedbacks in plant communities primarily at late successional stages. Using NGS metabarcoding, Stav Livne-Luzon *et al.* compared the ectomycorrhizal (ECM) community composition associated with the roots of young and mature *Pinus halepensis* and *Cedrus deodara* saplings. They found that host age determined the ECM community composition, raising questions about the species composition of ECM mycorrhizal inoculants for forest management applications.

The major knowledge gap on the role of multiple mycorrhizal types in dual and even triple hosts for AMF, ECM, and dark septate endophytes (DSE) was covered at ICOM11, a topic which has 'application' implications. Using meta-transcriptomics, Rytas Vilgalys *et al.* raised questions about the role of DSE interactions with other mycorrhizal types. Megan Ryan *et al.* showed that 'fine endophytes' (i.e., Mucoromycotina AMF), whose role in plant growth is remarkably poorly understood, are highly abundant in agricultural soils of southern Australia. Working in temperate forests in Europe, Fabian Weigl & Karin Pritsch showed that an abundance of unknown fungal taxa were

important to support the functioning of ECM under extreme drought. Taken together, these presentations underline that to achieve many mycorrhiza application goals we must gain a better understanding of all these different types of root-associated fungi.

Using mycorrhizal fungi to mitigate global change factors such as climate change, nitrogen deposition, shifts in fire regimes, and invasive species is a current hot topic, which ICOM11 captured. For example, Ruotong Zhao *et al.* and Nan Cui *et al.* showed that AMF can increase N mineralization under elevated temperature and N deposition, and significantly reduce N₂O emissions by enhancing *nosZ* gene (involved in denitrification) expression in soil. Martin Bidartondo called on the urgent need to understand how nitrogen deposition and consequent shifts in N:P ratios can affect mycorrhizal symbioses and their role on organic matter decomposition. Catherine Gehering *et al.* illustrated cumulative effects of climate change factors on mycorrhizal fungi with implications for forest restoration. Indeed, the development of mycorrhizal application practices should be based on data on how these symbioses can best function when exposed to multiple global stressors. Using species distribution models, Stephanie Kivlin *et al.* showed that AMF have much larger spatial ranges and niches than ECM, and that both of their niches are largely structured by main climate factors such as mean annual temperature. They concluded that since ECM are more restricted to cooler/drier habitats, they may be more susceptible to climate change than AMF (similar predictions were shown by Kabir Peay *et al.*), which is important in terms of forest management applications, particularly at higher latitudes and altitudes. Also on this topic, Wei Fu & Baodong Chen investigated AMF community responses to either chronic

or punctuated extreme drought in Inner Mongolia, signalling that only a few taxa are better suited to intense extreme drought events.

It is increasingly recognized that mycorrhizal function is intricately connected with the soil microbiome, a topic explored in presentations on climate change mitigation, agriculture, and environmental pollution. Jan Jansa drove this point across. In an elegant experiment using ^{15}N -labelled chitin as an organic N source, and modulating the presence/absence of AMF, bacteria, and protists under *in vitro* conditions, he showed that the presence of a specific prokaryote and protist in the hyphosphere can significantly boost N gains from organic sources by the AMF and their host plant. Lin Zhang *et al.* showed that AMF hyphae can recruit alkaline phosphatase-producing bacteria, which provides additional functions to the AMF symbiosis. Jiachao Zhou *et al.* investigated to what extent AMF traits may predict hyphosphere-bacteria associations, as they showed that *Gigaspora margarita* recruited more powerful soil organic P mobilizing bacteria and mobilized more P than *Rhizophagus intraradices* or *Funneliformis mosseae*. Another very interesting study highlighting the importance of bacteria-AMF interactions was presented by Nigkang Sun *et al.*, in which 3D printing was used to make a microfluid chip to test the mechanisms of chemotaxis involved in the recruitment of phosphate-solubilizing bacteria by AMF.

Trait-based approaches are increasingly useful to predict mycorrhizal functional outcomes. Bala Chaudhary *et al.* showcased a new framework adapted to specifically consider symbiotic functional outcomes of mycorrhizas. Alison Bennet *et al.* explored whether specific AMF traits (e.g., spore melanin content) could predict disturbance

and climate change factors, showing that certain traits can predictably respond to such factors. On plant traits, John Ramana *et al.* used NGS to identify AMF in the roots of 30 plant species along a gradient from fine to coarse roots. They found evidence for functional complementarity between roots and AMF traits, which predicted AMF identity colonizing plant roots. Taken together, the trait-based research presented at ICOM11 has important implications for improving mycorrhizal applications and is indicative of the way forward in the field.

Mushroom production for human consumption is a major application of mycorrhizas and ICOM11 included a session on this topic. Alexis Guerin-Laguette provided an overview of advances and challenges in cultivation reminding us that lack the necessary knowledge to produce many edible fungi commercially, including the “prestigious” Porcini, Matsutake, and Caesar’s mushrooms. Mara Rondolini *et al.* warned that natural areas in Italy where truffles have traditionally been found are declining and explored avenues to design conservation and restoration campaigns. Asunción Morte *et al.* analysed how ‘desert truffle’ (the ascomycete *Terfezia claveryi* that establishes ectendomycorrhizae with *Cistaceae*) is affected by abiotic and biotic factors, showing that high CO_2 concentrations help mycorrhizal hosts to cope with drought, and that *T. claveryi* is a heterothallic; relevant knowledge to develop new cultivation strategies.

MOLECULAR BIOLOGY

Johanna Wong-Bajracharya³ and Jonathan M Plett⁴

³Department of Primary Industries New South Wales, Australia. ⁴Western Sydney University, Australia.

Over the week of August 1-5, 2022, we had a wonderful time in ICOM11 & IMMM5 learning about the latest research in mycorrhizal molecular biology. Talks by various speakers have highlighted the significance of sequencing tools in advancing our understanding of molecular pathways involved in mycorrhizal symbiosis. For instance, keynote speaker Annegret Kohler's showed us an update on our understanding of the evolution of ectomycorrhizal (ECM) fungi through the lens of genomics and transcriptomics. During interaction with host roots, ECM fungi deploy diverse sets of carbohydrate-active enzymes (CAZymes); transporters or mycorrhiza-induced small secreted proteins (MiSSPs) were identified to be induced in different ECM fungal species, indicating independent evolution of ECM lineages. The talk by Benjamin Dauphin extended on this subject by demonstrating how our ever-growing access to multiple genomes within a given species of mycorrhizal fungi can be used for genome-wide association studies. In his work, he was able to show genes with significant correlation to ectomycorrhizal traits (e.g. host specificity) in the fungus model *Pisolithus microcarpus*. His work also shows the incredible genetic diversity between closely related isolates – a factor that we will need to increasingly consider when we are trying to understand the outputs of larger scale comparative genomics projects. Nicolas Corradi gave an excellent talk on similar research in arbuscular mycorrhizal (AM) fungi where they have gone to incredible depths

sequencing single nuclei to determine the level of genetic diversity each nucleus may bring to the functioning of the whole organism. Their ongoing work in this area has shown that the AM fungus model *Rhizophagus irregularis* may have a “two compartment” genome distinguished by different epigenetic markers whereby one set of genes is typically transcribed and another is typically repressed. While these results show intriguing parallels to work in mammalian models, there are distinct differences as effector-like genes found in both epigenetic states/genomic ‘compartments’, which are able to escape repression during host colonization. While comparative genomics have hugely increased our understanding of what characterizes a mycorrhizal genome, recent work comparing and contrasting mycorrhizal fungi with other lifestyles is also responsible for giving us a better understanding on the molecular pathways involved in the mycorrhizal symbiosis. Annie Lebreton presented her work comparing saprotrophic species and ECM species within the Russulales fungal order, and identified genes functionally related to ectomycorrhizal root tip development. In a complementary approach, Vidya Suseela has utilized mass spectrometry technology to profile plant metabolite changes during a mutualistic AM interaction in comparison to during a parasitic AM interaction. This comparison has indicated that organic acids and some flavonoids are required for a mutualistic AM symbiosis.

Over the week, we were also introduced to a range of exciting new developments in the molecular mechanisms involved in the establishment and functioning of AM and ECM symbioses. These talks continue to highlight the number of instances of convergent evolution that have led to the mycorrhizal symbiotic lifestyle, but also point

recent updates in research being conducted on protein signals used by mycorrhizal fungi during symbiosis formation. Claire Veneault-Fourrey talked about her findings on the newly characterised MiSSPs essential to kickstarting ECM symbiosis. Similarly, using *Laccaria bicolor* as a model, Feng Zhang's talk has demonstrated the importance of mycorrhiza-induced CAZymes in cell wall remodelling during ECM symbiosis formation through a series of RNAi and *in situ* localization experiments. During the iMMM5 talks, Sebastian Schornack discussed new work regarding effector candidates in the AM fungal symbiosis, and the discovery of AM fungal FOLD effector candidates. These FOLD dual-domain (FOLD) class of effector proteins, recently described in *Fusarium oxysporum*, may play a role in host recognition of the invading fungus. Intriguingly, Sebastian indicated that this class of effectors was not found within ECM fungi, suggesting a unique mode of action in AM fungi.

With regards to nutrition during symbiosis, Katsuharu Saito's talk has presented us with new evidence on the role of the fatty acid myristate as an energy and carbon sources used by AM fungi. Toby Kiers presented her recent work advancing our understanding of real time movement of nutrients within AM fungi using a variety of cutting-edge microscopic and molecular techniques to further develop predictive modelling to understand the cues that affect nutrient trading between the fungus and its hosts. Conversely, within ECM fungi, Krista Plett demonstrated how nutrient trading dynamics appear to be regulated differently than in AM fungi. As opposed to AM fungi, where market theory appears to be driving much of the nutrient trading dynamics, in ECM fungi Krista showed evidence for tight nutrient trade control on the part, and need, of the fungus. This control has both genetic and abiotic

bases, leading to an increasingly complex set of factors needing to be understood before predictive models can be built in these fungal lineages. Adding to the broader understanding of mycorrhizal symbioses, Silvia Perotto et al. discussed their work with the orchid mycorrhizal fungus *Tulasnella calospora*. In this obligate symbiosis, Silvia's group utilised laser dissection of colonized *Serapias* protocorms to identify nutritional networks at play. Surprisingly, the sulfur pathway appears to be one of the major nutrient pathways regulated. She also presented their work on transcriptomic characterization of symbiosis in other orchid mycorrhizal tissues taken from the field. This work showed some very interesting results in how we can begin bridging fine scale molecular results taken from controlled lab conditions and extrapolating and validating them under more natural conditions.

Altogether, across this week we saw how our molecular understanding of the evolutionary processes that led to the mycorrhizal lifestyle, and the mechanisms in host plants necessary to support mutualism, continue to make great strides. We are excited to see the development of these, and new, projects in the next ICOM/iMMM!

For general questions or suggestions,
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Highlights from the Ecological Society of America – Canadian Society for Ecology Evolution Joint Meeting, 2022

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Long gone are the days when presentations on mycorrhizas were crammed into a single session titled 'Mycorrhizae'. At this year's joint meeting between the Ecological Society of America (ESA) and the Canadian Society for Ecology Evolution (CSEE), there was one symposium ('Trait-based approaches in fungal ecology: where are we, and where next?'), one organized session ('Mycorrhizal associations and climate change'), three contributed sessions ('Mycorrhizae' 1–3), and over a dozen other sessions containing talks focused on mycorrhizas. No longer is research on mycorrhizas siloed; it is clear that researchers from various disciplines recognize mycorrhizas' importance in understanding processes across ecological scales. Across posters and talks, there were over 100 presentations focused on mycorrhizas. The research presented in this year's meeting matched the set theme 'A change is gonna come'. From carbon cycling to fungal community response to events such as drought, tree species migrations, and glacial retreat, mycorrhizal research was rooted in the reality of changing environments. Below, we highlight several themes and relevant presentations that were particularly innovative in moving the needle in mycorrhizal ecology.

After more than a decade of trying to link fungal identity to function using next

generation sequencing technology such as Illumina Mi-Seq along with ecological function databases such as FUNGuild (Nguyen *et al.* 2016), ecologists are increasingly looking at trait-based approaches to develop greater predictive capabilities. Pierre-Luc Chagnon (Université de Montréal) organized an excellent symposium on fungal traits with presentations by Bala Chaudhary, Justine Karst, Pierre-Luc Chagnon, and Hiba Benmohamed. Chaudhary, Chagnon, and Benmohamed gave thought-provoking theoretical talks aimed at guiding trait research in the coming years, and Karst relied on traits associated with exploration type of ectomycorrhizal (EM) fungi to make a case that EM fungi are more than just functional extensions of tree roots. That is, EM fungi seem to respond to changes in carbon allocation rather than the nutrient demands of the tree.

Large databases are now contributing to studies that can lead to a more predictive ecology regarding biogeography and invasions. Using the Global Naturalized Alien Flora (Pyšek *et al.* 2017; van Kleunen *et al.* 2019) and the Global Inventory of Floras and Traits v 1.0 (Weigelt *et al.* 2020) databases, Camille Delavaux *et al.* showed evidence that the mycorrhizal type of the hosts is a strong environmental filter for colonization on

islands, and that the more remote the island, the stronger the filtering. They found that native arbuscular mycorrhizal (AM) plant species on islands made up a lower proportion of plant species relative to mainlands. However, humans appear to be relaxing this filter on islands; naturalized floras had higher proportions of AM plant species than native floras. Using a combination of data from *FungalRoot* (Soudzilovskaia *et al.* 2020) and the United States Department of Agriculture's Forest Inventory Analysis database (Gray *et al.* 2012), Corrina Thomsen & Jason Pither tested two predictions emerging from plant-soil feedback concept: 1) the abundance of canopy EM tree hosts is positively correlated with the abundance of EM host plants in the understory, and 2) the abundance of canopy AM tree hosts is negatively correlated with the abundance of AM host plants in the understory. Results were consistent with their predictions highlighting the important role understory plants may have on the mycorrhizal dynamics in natural forest ecosystems.

Investigating the effect of tree mycorrhizal type on a range of properties in forest stands was definitely going strong at ESA, but the need for recognizing additional mycorrhizal types is emerging. Similar to Thomsen & Pither, Elisabeth Ward *et al.* recognized that forest function is not just contingent on the mycorrhizal type of trees, but also depends on the mycorrhizal type of plants growing beneath the tree canopy. Ward *et al.* tested whether the influence of ericoid shrubs on soil biogeochemistry would either extend or be redundant with that of EM trees. They found that ericoid plants strongly modulated tree mycorrhizal dominance effects. The relative basal area of EM trees was negatively associated with soil carbon and nitrogen concentrations in the soil, but these

relationships were weak to negligible in the absence of ericoid plants. Importantly, they suggest 'that [ericoid] shrubs could confound interpretation of AM versus EM tree effects in forests where they co-occur and that this could have implications for predicting forest biogeochemical processes at the global scale'. Along these same lines, functional differences among species of EM fungi may make a singular assignment of trees as 'EM' questionable. This issue was highlighted in the results of a novel study by Talia Michaud *et al.*, where they measured nitrogen concentration and $\delta^{15}\text{N}$ in herbarium specimens of EM and non-EM plants and fungi collected from 1871–2016. Based on tissue samples (foliar and sporocarps), EM symbionts were less sensitive to declining nitrogen availability over the time period compared with non-EM symbionts. However, of the four EM fungal genera sampled, only *Tricholoma* showed an increase in $\delta^{15}\text{N}$, consistent with the hypothesis of increased access to nitrogen bound in soil organic matter. The stable isotope signatures of the other EM fungal genera, *Amanita*, *Laccaria*, and *Scleroderma*, were more in-line with those of the sampled saprobes, *Lycoperdon*, *Marasimius*, and *Psathyrella*. This means that EM trees may be buffered from changes in nitrogen availability depending on the species of fungi with which they form associations. These results point to a spectrum of function possibly masked within a single mycorrhizal type, and the need to apply mycorrhizal type categories more carefully.

Understanding the ecology of mycorrhizas in dual-hosts was another emerging theme at the ESA-CSEE meeting. Ecologists are puzzled as to why some plant hosts harbor multiple mycorrhizal types and recognize that understanding what drives interactions between EM and AM fungi may be important for predicting forest responses to global

change factors. Elena Schaefer *et al.* presented a field study on the dual-host *Populus fremontii*, a tree species common in the arid southwest region of USA, and found the amount of carbon exuded from fine roots was very low and independent of the extent of EM and AM root colonization. They concluded that contrary to trees evaluated mostly in temperate regions, *P. fremontii* conserves carbon by limiting the amount of carbon released from fine roots. In another study examining dual-hosts, Kathleen Thompson *et al.* tested whether co-colonization of AM and EM fungi on roots of *Populus deltoides* depends on nitrogen source, soil moisture, and light intensity. They found that the ratio of EM: AM colonization can be explained by nitrogen and an interaction between nitrogen and light. EM colonization is more abundant when nitrogen is limited and when light is not limiting.

Talks and posters alike linking mycorrhizas and other trophic levels were common at this year's conference. The influence of mycorrhizas on belowground processes is well-studied, yet it is often isolated from soil food webs. Emerging research by Janey R. Lienau *et al.* sought to understand how traits of mycorrhizal trees shaped macroinvertebrate communities found in the understory of forests. Combining mycorrhizal type (AM or EM) with leaf habit (evergreen or deciduous), their results show that while AM trees harbor more abundant soil invertebrates, EM trees have a more specialized set of macroinvertebrate community members. The extent to which each mycorrhizal type predicted species abundance and diversity was also correlated with leaf habit, elucidating that the interaction between environments structured by both host and fungi can shape other trophic levels within the soil. Matthew L. Reid *et al.* examined how microarthropods influenced AMF abundance in soils of

bioenergy crops. When soil fauna were added to mesocosms, AM extraradical hyphal length increased, highlighting that microarthropods may promote AMF abundance in the soil of bioenergy cropping systems, with potential carbon accrual benefits. Aboveground, Aidee Guzman *et al.* investigated how AMF mediate floral traits and impact pollinator dynamics. Using complementary field and greenhouse experiments, their work linked AMF richness and functional diversity with pollinator behaviors, such as the number of times bees visited each flower or visitation time. Moreover, by leveraging traits, this study revealed that flower size, an important factor in bee visitation rates, depends on AM functional traits, including hyphal length and root colonization.

Finally, as mycorrhizal researchers, we often plead with people in other fields to stop ignoring the belowground in ecology. However, the study by Rebecca Snell *et al.* was a reminder of the importance of above- and belowground processes in mycorrhizal ecology. They leveraged a 10-year experiment in an oak-hickory forest where lime had been added to raise soil pH, and in consequence, nitrogen availability. In control plots, stem radial growth did not differ between EM and AM trees, however, in the limed plots, AM trees had higher growth rates than EM trees. To further understand the long-term impacts of liming on forest composition and dynamics, they assessed its impact on AM and EM seedling density. Arbuscular mycorrhizal seedling density increased with liming, however, EM seedling density decreased. Naturally, we would look to belowground mechanisms to explain this result. However, liming also affected tree reproduction. Arbuscular mycorrhizal trees produced many more seeds than EM trees. At first glance, it appeared that soil conditions filtered seedling establishment depending on

mycorrhizal type, however, upon further examination, it seems that seed inputs likely caused the difference in seedling survival. The importance of evaluating alternative hypotheses was noteworthy and are always important to keep in mind!

We look forward to watching how these themes in mycorrhizal ecology develop over the next conference season!

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Research commentaries

Trait-based approaches in arbuscular mycorrhizal fungi need to distinguish between response and effect traits

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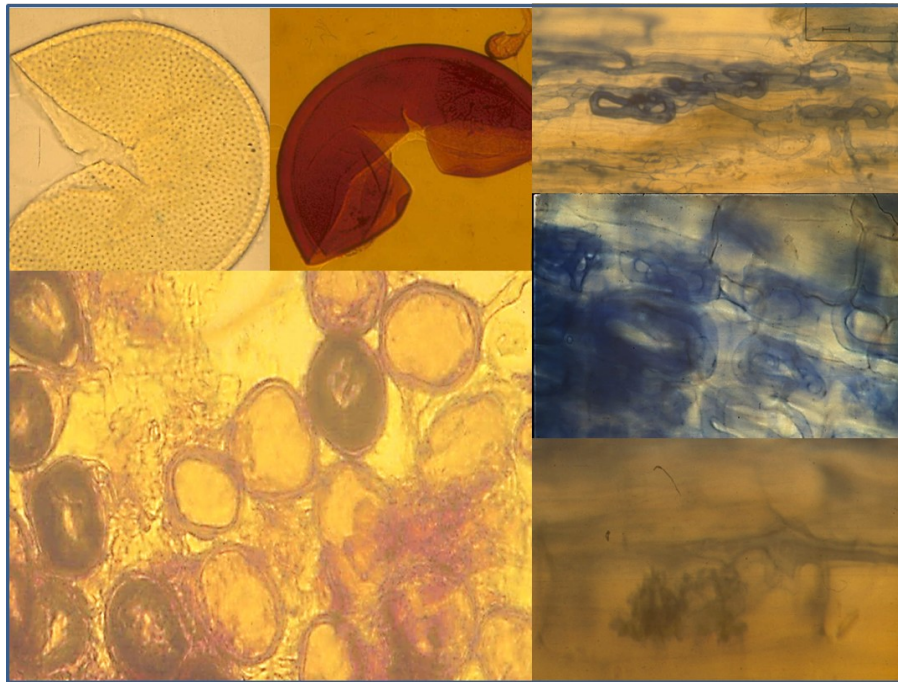
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Mycologists usually borrow models or theoretical frameworks from other ecological disciplines to test them in fungal ecology. For example, using models from plant and animal ecology, some attempts intended to classify fungi according to life-history strategies, or functional groups and guilds (Pugh 1980; Urcelay and Robledo 2004; Zanne *et al.* 2019). In this way, species composition in a community is simplified to a few groups or guilds of species sharing similar traits from which we can make some predictions about nature functioning. Importantly, these classifications could be based on “response” traits to environmental changes or “effect” traits on ecosystem processes, and classifications based on response traits could differ from those based on effect traits (Díaz and Cabido 2001; Lavorel and Garnier 2001).

Although there is a large number of studies on the effects of arbuscular mycorrhizal fungi (AMF) on plant nutrition and growth, and even on the composition and productivity of plant communities, we still do not have a clear understanding of the differences in the symbiotic efficiency between species or groups of species in different contexts. Some studies have proposed that developmental traits (as the production of intra- and extraradical hyphae), regenerative traits (as spore size and abundance), and phenology, are phylogenetically conserved (Hart and Reader 2002; Chagnon *et al.* 2013). Therefore,

AMF taxonomic groups in a phylogeny-based classification would roughly correspond to functional groups or guilds based on those traits. Thus, if we know the taxonomic composition of the AMF communities, we can predict their response to the biotic and abiotic environmental changes and their effects on plant communities and ecosystem processes (Van der Heijden and Scheublin 2002; Chagnon *et al.* 2013; Weber *et al.* 2019; Davison *et al.* 2020). In addition, it has been recently proposed a trait-based framework that expands this perspective by considering other traits and distinguishing between plant, fungal, and symbiotic mycorrhizal traits (Chaudhary *et al.* 2022). A common feature of most trait-based frameworks and functional classifications of AMF is that they frequently do not distinguish between response and effect traits. Instead, they indistinctly referred to “traits” and therefore, the proposed groupings do not distinguish between response and effect groups or guilds.

The results of the literature instead show that the traits that might be useful to postulate AMF functional response groups to environmental changes are not useful to postulate AMF functional effect groups on the performance of plants and/or soil processes. For instance, it has been observed that Gigasporales are more sensitive to disturbances such as land use while Glomerales are more resistant or even



Structures from different Glomeromycota species. By: Nicolás Marro.

favoured (e.g. Jansa *et al.* 2003; Longo *et al.* 2016; Cofré *et al.* 2017). In turn, the Diversisporales, specifically Acaulosporaceae, showed to be more resistant to some stressful conditions such as low pH and low temperatures (Jansa *et al.* 2014; Davison *et al.* 2021). These findings are roughly in line with the above mentioned models. In contrast, a recent meta-analysis showed that the effects of those taxonomic groups on plant performance were not aligned with the predictions derived by the functional classifications based on taxonomic groups (Marro *et al.* 2022). For example, while Gigasporales are predicted to have greater efficiency in plant nutrition (Chagnon *et al.* 2013; Weber *et al.* 2019), the meta-analysis showed that they are more efficient in reducing the adverse effects of biotic stress such as defense against herbivores and pathogens. In turn, Diversisporales (including Acaulosporaceae) have the greatest benefits on plant nutrition and growth under regular conditions (i.e. without stress). A remarkable result that arises from that study is that only a few species of most groups have been studied, which indicates that the knowledge

we have built on this subject could be biased toward those few species (Marro *et al.* 2022).

In our opinion, we might be facing similar challenges that plant ecologists faced a couple of decades ago: the need to recognize traits useful to construct response groups (or guilds) and traits useful for effect groups (Díaz and Cabido 2001; Lavorel and Garnier 2001). In AMF ecology, the evidence thus far, suggests that traits that respond to environmental changes seem not to be the same as those that explain the effects on plant performance and/or ecosystem processes. For instance, the greater extraradical mycelial production and lower spore production that could be related to a higher susceptibility of Gigasporales to soil disturbances do not seem to provide greater access to soil P (and thus higher plant nutrition), as has been suggested based on some evidence (e.g. Chagnon *et al.* 2013). In turn, these traits could be related to soil aggregation (Van der Heijden and Scheublin 2007; Rillig *et al.* 2015), but this remains to be tested. On the other hand, the higher intraradical colonization and spore

production in Glomerales would make this group more resistant to disturbances but not provide greater root protection from plant pathogens or herbivores as has been previously proposed (e.g. Chagnon *et al.* 2013). Apparently, we are still far from knowing which are the traits through which AMF provide different benefits to plants. But what we know is that they are probably not the same as those related to their response to environmental changes.

As has been recently asserted in a previous article in this Newsletter, the ecology of AMF based on functional traits is still in its infancy (Chagnon 2022). There are many AMF species or groups of species that have been little studied or have not been studied at all (Van der Heijden and Scheublin 2007; Chagnon 2022; Marro *et al.* 2022). Therefore, the number of studied species must increase, particularly in those phylogenetic groups that have been poorly studied. This will allow testing for the generality of trait phylogenetic conservatism in AMF and provide more solid bases for assimilating taxonomic groups with functional groups or guilds (Chagnon 2022). In addition, trait-based frameworks should be more inclusive, considering a greater number of traits (Chaudhary *et al.* 2022). Last but not least, trait-based frameworks and functional classifications need to distinguish between "response" and "effect" traits, and within the latter, those that are related to the effects on plant performance and those that affect soil processes. Only after that, the challenges will lie in trying to link functional response groups with functional effects (Lavorel and Garnier 2001) in order to understand the functional diversity maintaining ecosystems functioning.

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Mycorrhizal fungi in the waiting room: fungal associations in Orchidaceae shed light on mycorrhizal evolution.

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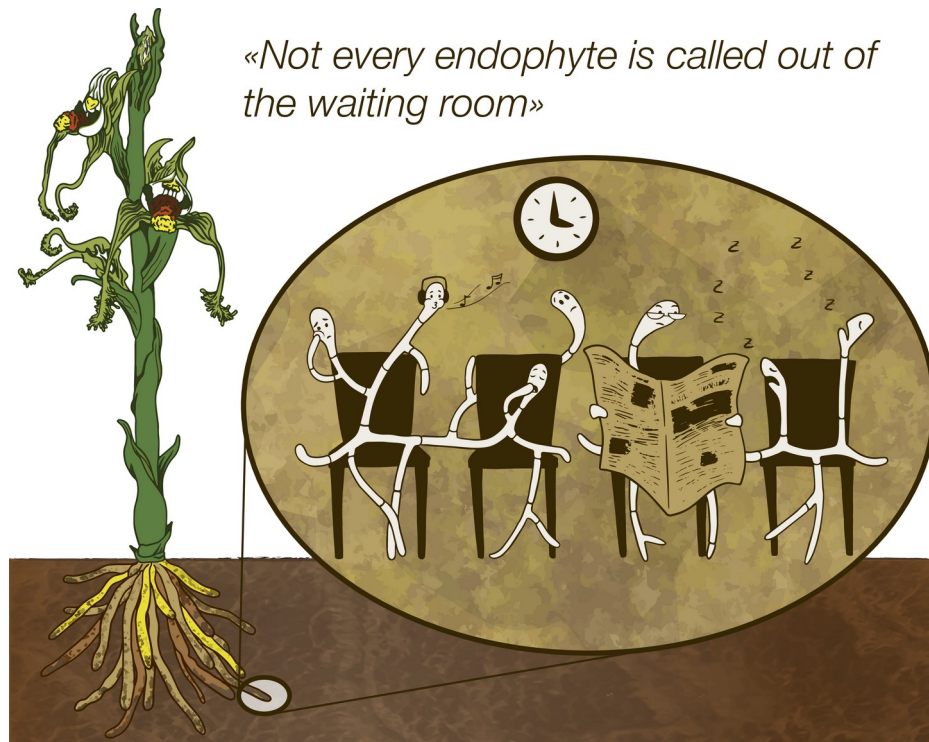
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One of the main goals in the study of mycorrhizas is to understand the evolution of fungal mycorrhizal habit, a transition that occurred many times across the fungal phylogeny (Kohler *et al.* 2015). One recognized hypothesis is that mycorrhizal fungi repetitively evolved from saprobic ancestors, which has received strong support from fungal phylogenomics (Kohler *et al.* 2015; Miyauchi *et al.* 2020; Looney *et al.* 2022). Transitions from saprotrophy to symbiosis have involved several genomic modifications that are observed across lineages, for example, the widespread losses of degrading enzymes acting on lignin and cellulose, and the diversification of novel, lineage-specific symbiosis-induced genes (Miyauchi *et al.* 2020).

Recently, another scenario for the evolution of fungal mycorrhizal lifestyle was suggested by the “Waiting Room Hypothesis” (WRH). This hypothesis postulates that in many cases, mycorrhizal habit might have evolved from root endophytism. Mycorrhizal associations imply, for both partners, (1) morphological modification(s) to build the mycorrhiza, and (2) more elaborated and intense nutrient exchanges than in endophytism. The WRH proposes that root endophytes, *i.e.* fungi that colonize roots and do not entail morphological symptoms nor differentiation of one or the other partner (Rodríguez *et al.* 2009) are predisposed to become mycorrhizal, since they occupy an ecological

niche that allows the transition to tighter associations with the host. Following this hypothesis, root endophytism acts as a symbiotic ‘waiting room’, where biotrophic coexistence predisposes evolution towards mutualism with a more complex joint mycorrhizal morphogenesis (Selosse *et al.* 2018).

The WRH predicts two features. First, that after the evolutionary transition to mycorrhizal status occurred, the fungus that is now mycorrhizal in a given plant lineage may have retained endophytic abilities in other plant lineages, and thus has a dual niche. This endophytic presence is especially expected in plants phylogenetically closer to the ones that are mycorrhizal. Second, given that the mycorrhizal habit is expected to be a derived trait, the mycorrhizal lineage arises phylogenetically among earlier-diverging lineages that are endophytic. This pattern has been observed for example, in the Sebaciales, which repeatedly evolved orchid, ectomycorrhizal, and ericoid mycorrhizal habits from endophytic ancestors (Weiß *et al.* 2016). It occurs in some saprobic species of the genus *Mycena* which are also known to be endophytic and also occur as mycorrhizal fungi in orchids (Selosse *et al.* 2010) or in Ericaceae (Grelet *et al.* 2017). In a recent article published in *Ann Bot* (Selosse *et al.* 2022), we examined the fungal associations in Orchidaceae from an evolutionary perspective, in order to test the WRH.



Orchids belong to Asparagales, which form arbuscular mycorrhizas with Glomeromycota (Smith and Read 2008). However, most orchids, including the most anciently diverging lineages, associate with rhizoctonias - a polyphyletic group formed by the basidiomycetous families Serendipitaceae, Ceratobasidiaceae, and Tulasnellaceae (Dearnaley *et al.* 2012). This suggests that the last common ancestor of extant orchids was probably mycorrhizal with rhizoctonias, as was also supported by the reconstruction of ancestral states (Wang *et al.* 2021). Thus, orchids abandoned Glomeromycotinas and shifted to a mycorrhizal association with rhizoctonias.

Besides being mycorrhizal, rhizoctonias are free-living soil saprobes that decompose organic matter, as they have been shown to grow on plant decaying material (Smith and Read 2008), and have large enzymatic capabilities (Miyachi *et al.* 2020). Yet, they are also endophytes in non-orchid plants! For example, *Serendipita* (= *Pyriformospora*) *indica* is a well-studied model of plant endophyte that is also orchid mycorrhizal. Members of

Tulasnellaceae are endophytic, e.g. in *Euphorbia* spp. and *Bromus erectus*, and although many Ceratobasidiaceae are parasitic in non-orchid roots, some species are symptomless and endophytic (see references in Selosse *et al.* 2022). Thus, rhizoctonias are saprobic and endophytic in non-orchid roots. As expected under the WRH, this permissive ecology may be a predisposition to evolve mycorrhizal abilities, not only in the ancestors of orchids but also in other plant groups. Indeed, some rhizoctonia lineages were also recruited in other mycorrhizal types: ectomycorrhizal associations arose in the three families of rhizoctonias, and members of Serendipitaceae were also recruited as ericoid mycorrhizal fungi (see references in Weiß *et al.*, 2016 and Selosse *et al.* 2022). Thus, endophytism in rhizoctonias likely allowed the transition to ectomycorrhizas and to coil-forming mycorrhizas (orchid and ericoid mycorrhizas), as expected by the WRH.

Besides the association with rhizoctonias, some orchid species have shifted partners from rhizoctonias to ectomycorrhizal fungi.

The symbiosis with these new partners is linked to the physiological ability to extract carbon compounds from the fungus. Some of these orchids use the fungus as an exclusive carbon source and are therefore mycoheterotrophic, whereas others use fungal carbon in addition to autotrophy, known as mixotrophic orchids (Smith and Read 2008; Dearnaley *et al.* 2012). Such transitions of partners and nutritional physiology occurred convergently in orchid evolution (Wang *et al.* 2021). Interestingly, ectomycorrhizal fungi are frequently detected at low frequencies in roots of fully photosynthetic rhizoctonia-associated orchids (in at least 54 species throughout the phylogeny of the orchid family, based on 42 studies; see Table 1 in Selosse *et al.* 2022). Probably these taxa are present as endophytes, which is supported by the growing evidence that some ectomycorrhizal fungi colonize the roots of non-ectomycorrhizal plants as endophytes (Selosse *et al.* 2018). The presence of these fungi as endophytes in ancestral green orchids and as mycorrhizal in derived non-fully autotrophic lineages is predicted by the WRH.

Finally, there are some orchids that shifted from rhizoctonias to saprobic fungi, also associated with the transition to mycoheterotrophy. Like what is observed with ectomycorrhizal fungi, saprobic fungi are also present at low frequencies in roots of rhizoctonia-associated green orchids (in at least 15 species throughout the phylogeny of the orchid family, based on 15 studies; see Table 2 in Selosse *et al.* 2022). In both cases, ectomycorrhizal and saprobic fungi present as endophytes in roots of green orchids, are available -in the waiting room- to be recruited to evolve mycorrhizal interaction, as expected under the WRH.

Selosse *et al.* (2022) compiles evidence that supports the hypothesis that the diverse orchid mycorrhizal associations (from the ancestral rhizoctonias to the various derived fungal partners) are based on the evolutionary recruitment of endophytes that became mycorrhizal, following the WRH. The waiting room hypothesis arose in the face of an accumulative evidence of dual niches in fungal species, allowed by the increasing trend to report the whole fungal communities detected in roots. Thus, we believe that the interest in describing microbiota diversity more comprehensively, will provide new evidence to further test the range of application of the waiting room hypothesis.

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YouTube interviews*

- Jonathan Plett on effector proteins in fungi

Camille Truong interviews Jonathan Plett, Professor at Western Sydney University, who discusses how fungal effector proteins on colonization and nutrient acquisition and cycles.

Interview: <https://southmycorrhizas.org/reading/may-2018/july-ii-2022/>

Study: Plett JM, Plett KL. 2022. Leveraging genomics to understand the broader role of fungal small secreted proteins in niche colonization and nutrition. *ISME Commun* 2:49. <https://doi.org/10.1038/s43705-022-00139-y>

- Johanna Wong-Bajracharya, ICOM11 student award winner, on ectomycorrhizal microRNAs

César Marín interviews Johanna Wong-Bajracharya, a recent student award winner at ICOM11, on how ectomycorrhizal microRNAs control host gene expression.

Interview: <https://southmycorrhizas.org/reading/october-2022/>

Study: Wong-Bajracharya J, Singan VR, Monti R, *et al.* 2022. The ectomycorrhizal fungus *Pisolithus microcarpus* encodes a microRNA involved in cross-kingdom gene silencing during symbiosis. *Proc Natl Acad Sci USA* 119:e2103527119.

<https://doi.org/10.1073/pnas.2103527119>

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South American Mycorrhizal Research Network

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Tools

→ Mycelium chemistry differs among mycorrhizal types

While not strictly a tool, Huang *et al.* (2022) demonstrated that the chemical composition of arbuscular mycorrhizal (AM) and ectomycorrhizal (EM) fungi differs greatly, as EM mycelium has higher concentrations of labile and recalcitrant components, while AM mycelium contains more acid-hydrolysable components. This insight into mycorrhizal decomposability traits can help us to better understand the carbon cycle.

Study: Huang W, van Bodegom PM, Declerck S, *et al.* 2022. Mycelium chemistry differs markedly between ectomycorrhizal and arbuscular mycorrhizal fungi. *Commun Biol* 5:398. <https://doi.org/10.1038/s42003-022-03341-9>

→ *In vitro* tripartite mycorrhizal associations and bacterial biofilms

Pandit *et al.* (2022) created an *in vitro* assay, based on synthetic growth in a two-compartment Petri plate system, to recreate functional biofilms with AMF-associated bacteria. Such biofilm increased the sporulation of *Rhizophagus irregularis*. They found that mycorrhizal/bacterial interactions in the biofilm influenced the functionality of both partners.

Study: Pandit A, Johny L, Srivastava S, *et al.* 2022. Recreating *in vitro* tripartite mycorrhizal associations through functional bacterial biofilms. *Appl Microbiol Biotechnol* 106:4237-4250. <https://doi.org/10.1007/s00253-022-11996-x>

→ A framework for the use of AMF inoculants

Given recent and not-so-recent studies and meta-analysis that show that AMF-based inoculants have inconsistent product efficacy, Salomon *et al.* (2022) propose a quality management framework to improve their quality, use, and efficacy. This framework includes aspects regarding composition, viability, bioassays, packaging, and carrier material.

Study: Salomon MJ, Watts-Williams SJ, McLaughlin MJ, *et al.* 2022. Establishing a quality management framework for commercial inoculants containing arbuscular mycorrhizal fungi. *iScience* 25:104636. <https://doi.org/10.1016/j.isci.2022.104636>

→ Labelling techniques to elucidate resource transport in AMF

Watts-Williams (2022) reviews the literature regarding the use of stable or radioactive isotope labelling to elucidate the mycorrhizal uptake pathways. How different nutrients (phosphorous, nitrogen, zinc, carbon) are transported in mycorrhizas is a critical question in mycorrhizal research. This review gives an overview on labelling techniques and how they can inform about mycorrhizal functioning under climate change and sustainable management.

Study: Watts-Williams SJ. 2022. Track and trace: how soil labelling techniques have revealed the secrets of resource transport in the arbuscular mycorrhizal symbiosis. *Mycorrhiza* 32:257-267. <https://doi.org/10.1007/s00572-022-01080-7>

Click for previous Tools: [Vol1_I1](#) (p. 11), [Vol1_I2](#) (p. 15), [Vol1_I3](#) (p. 16), [Vol2_I1](#) (p. 19), [Vol2_I2](#) (p. 15), [Vol2_I3](#) (p. 15), [Vol3_I1](#) (p. 16), and [Vol3_I2](#) (p. 17).

Events

MYCORRHIZAL EVENTS:

III International Symposium on Mycorrhizal Symbiosis in South America

[Website](#)

Instituto SINCHI, Leticia, Colombia

24 August – 2 September, 2023

Organizers: South American Mycorrhizal Research Network and Instituto SINCHI



OTHER EVENTS:

- 45th *New Phytologist* Symposium: Ecological and evolutionary consequences of plant–fungal invasions

[Website](#)

Campinas, Brazil

Date not yet announced

Organizers: New Phytologist Trust and symposium organizers.

- 10th International Symposium on Forest Soils - ISFS 2022

[Website](#)

Zhijiang Hotel, Hangzhou, China

17 – 21 October, 2022

Organizers: Zhejiang A&F University and others



- 3rd Global Soil Biodiversity Conference

[Website](#)

Clayton Hotel, Dublin, Ireland

13 – 15 March 2023

Organizers: Global Soil Biodiversity Initiative



GLOBAL
SOIL BIODIVERSITY
INITIATIVE

III Argentinian Mycology Meeting

[Website](#)

Universidad Nacional de Córdoba, Córdoba, Argentina

17 – 21 October, 2022

Organizers: Universidad Nacional de Córdoba & Asociación Micológica Carlos Spegazzini



ANNOUNCEMENTS

IMS Announcement.

Dear IMS members,

It is with great joy that I am pleased to announce that Twitter and Instagram accounts have been created for the IMS. Also, the Facebook account will be more active from now on. In these accounts, we will share information about mycorrhizal basics, research, mycorrhizologists, and much more. The content will be developed not only for people knowledgeable in the subject but also for anyone interested in mycorrhizal symbiosis. I also have two announcements to share:

1. People interested to join the IMS Communications Team: This is primarily a call for students interested to communicate about mycorrhizas, but is open to anyone who is enthusiastic about participating. I also ask you to please encourage your students to be part of this team. To apply please send me a 500-word letter explaining why you want to be part of the communications team and a short one-page CV. Deadline: November 14, 2022.
2. For IMS members we offer the Twitter, Instagram and Facebook accounts to promote events of interest and job openings. I would also like to invite you to send pictures and descriptions of mycorrhizal science outreach activities that you did or will do in order to enhance our work with the community.

To send the information for both announcements please send an e-mail to psilva@ucm.cl

I look forward to hearing from you and please follow us on:

Twitter/Instagram: [@mycorrhiza_ims](https://twitter.com/mycorrhiza_ims)

Facebook: [@internationalmycorrhizasociety](https://www.facebook.com/internationalmycorrhizasociety)

Patricia Silva-Flores - IMS Communications Director

SPUN Announcement: Underground Explorers Program: Call for Applications.

SPUN (Society for the Protection of Underground Networks) is a scientific research organization founded to map mycorrhizal fungal communities and advocate for their protection. We aim to create a diverse community interested in exploring mycorrhizal fungi around the world. We created the Underground Explorers program to help fund research that explores global patterns of mycorrhizal fungal diversity. Here we present our first call for applications.

Information on deadlines, funding, preferred locations, etc. on:

<https://www.spun.earth/expeditions/apply>

About the artwork for the current issue cover.

Special thanks to Dr. Besiana Sinanaj from the University of Sheffield for providing us her outstanding artwork for our cover. Besiana will soon launch her company "Besiana LTD", which will be selling and commissioning her original artwork, prints, products, and scientific illustrations. Follow Besiana in Twitter at: [@BesianaX](https://twitter.com/BesianaX)

IMS Newsletter

Editor-in-Chief: Prof. Dr. César Marín, Center for Research and Innovation for Climate Change, Santo Tomás University, Chile (cmarind@santotomas.cl).

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ICOM12 will be organised in the summer of 2024 in Manchester, United Kingdom, by Prof. Dr. David Johnson (University of Manchester) and colleagues.