Mycorrhizae for a sustainable world

Article

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The 10th International Conference on Mycorrhiza (ICOM10), Mérida, Mexico, June 30 – July 5 2019

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Meeting report

More than 80% of plant species exchange resources with mycorrhizal fungi and these associations impact both partners at multiple scales, from individuals to ecosystems. 172 participants from 33 countries and 160 institutions met at the 10th International Conference on Mycorrhiza in the city of Mérida in the Yucatan peninsula in Mexico – an area famous for its Mayan archaeological sites, cenotes, and the Chicxulub impact crater that marks the end of the Cretaceous period. They discussed latest advances on mycorrhizal research across 125 talks and 111 posters in 14 sessions focused on the biology, physiology, ecology, evolution and conservation of these interactions from molecules to biomes (Fig. 1). In particular, the contribution of mycorrhizal research to sustainability in agriculture, conservation and ecosystem restoration (Fig. 2) emerged as a promising topic to address today's challenges in the realm of human population growth, globalization and climate change.

1. Sustainability in agriculture (managed ecosystems)

Several speakers discussed the increasing abundance of commercial arbuscular mycorrhizal products for agriculture, from "biofertilisers" to advances in seed coating technology (i.e. adding mycorrhizal fungal spores directly to seeds along with nutrients and plant-helper bacteria), and the interest in these products from growers.

A noticeable recurring theme was that commercial biofertilisers make rather dramatic claims about their effectiveness, without evidence of their application leading to direct improvements in crop yield or nutrition. Jan Jansa (Czech Academy of Sciences, Prague, Czech Rep.)'s keynote presentation made the point that biofertilisers do not *create* nutrients per se; however, they may help plants to access existing nutrient sources, and may provide non-nutritional benefits. Examples of non-nutritional mycorrhizal benefits include increased soil glomalin inputs, tolerance of microplastics inputs, and alteration of the soil microbiome (Svenningsen *et al.*, 2018; de Souza Machado *et al.*, 2019; Hestrin *et al.*, 2019). Marcel van der Heijden (Agroscope, Zurich, Switzerland) and Ashleigh Elliott (University of Leeds, Leeds, UK) presented data on the application of commercial inoculants in field and glasshouse trials; crops grown with a commercial arbuscular mycorrhizal (AM) fungal inoculant exhibited higher root colonisation but there were few benefits to growth. Notably, the quality (in terms of active AM fungal propagules) and effectiveness of different commercial products was highly variable.

Miranda Hart (University of British Columbia, Kelowna, Canada) made the case that the variable responses of AM fungal inoculum in field trials are like those observed in the case of plant species invasions (Thomsen & Hart, 2018), and that current practices were too focused on establishing the most vigorous AM fungi. Some important questions arose from the workshop discussion on the topic: how can we, as a research community, contribute to ensuring that mycorrhizal fungal inoculum products are a) appropriate, e.g. are we selecting the most suitable fungi for a given system, rather than good invaders?; and b) successful, e.g. would a "certificate of effectiveness" be required?

In terms of alternative approaches to agriculture, Rillig & Lehmann (2019) identified approximately 285,000 combinations of agricultural practices. In his keynote, Jan Jansa emphasised the need to rigorously quantify the AM symbiosis and its effects in the field, to enable the production of equations and models that make useful predictions, so that we can best make use of the AM symbiosis as a valuable biological resource. Jansa also highlighted the potential to look further down the production chain not only to crop productivity but to the quality of the food product (e.g. do mycorrhizas affect food nutritional content, taste, or spoilage), such as lowered pest impacts, postharvest disease reduction, and thus reduction of food waste (e.g. AM fungi for food security).

2. Sustainability in conservation and restoration (natural ecosystems)

Effective use of the mycorrhizal symbiosis for restoration and conservation requires a deeper understanding of mycorrhizal functionality and related ecosystem processes, and how these processes and functions are altered through interactions with other actors and changing conditions. For instance, several talks (e.g. Heike Bücking, South Dakota State University, Brookings, USA; Ricardo Arraiano Castilho, Kew Gardens, London, UK) highlighted the importance of local soil factors and host nutrient demand in shaping mycorrhizal fungal communities, and whether changes in local environmental conditions associated with climate change (i.e. drought) or nutrient deposition (i.e. soil fertility) may disrupt the structure of these communities. Many speakers discussed the contribution of mycorrhizas in low impact, sustainable approaches to ecosystem restoration (e.g. Brian Pickles, University of Reading, Reading, UK; Cameron Egan, University of Hawaiʻi, Mānoa, USA) and species conservation (e.g. Nicole Hynson, University of Hawaiʻi, Mānoa, USA; Louise Egerton-Warburton, Chicago Botanic Garden, Glenco, USA). Still, other mechanisms related to the activities of mycorrhizal fungi, such as carbon sequestration (i.e. priming effect discussed by María Pozo, EEZ-CSIC, Granada, Spain; and Johanna Pausch, University of Bayreuth, Bayreuth, Germany) or the outcome of interactions among important actors, such as signaling pathways for kin recognition (e.g. Monika Gorzelak, Agriculture and Agri-Food Canada, Lethbridge, Canada), need to be accounted for when considering mycorrhizal applications in conservation and ecosystem restoration.

A key theme is that different ecosystems may well need different approaches (i.e. there is no “silver bullet” for restoration or conservation). For example, Louise Egerton-Warburton found that “cedar” (*Widdringtonii wrighteii*) seedlings grew well in nursery conditions but experienced drastic mortality following transfer to the field in Malawi. In turn, Nicole Hynson and Cameron Egan’s work showed that incomplete recovery of Hawaiian native fungal communities following successful growth of planted native host trees may compromise forest restoration. However, the presence of diverse mycorrhizal fungal communities is not the only requirement for a successful restoration plan. For instance, when comparing the performance of AM fungal species on high- and low-quality (determined by associated fungal biomass) native plant hosts in tallgrass prairie, Ylva Lekberg (MPG Ranch, Missoula, USA) found that AM fungal identity and abundance influenced plant performance, while AM fungal species diversity was unimportant in this regard. Similar results were found in a successional plant-feedback study where only the appropriate late successional AM fungi with their corresponding plant species grew faster and larger (Koziol & Bever, 2019). In the North American Southwest, Catherine (Kitty) Gehring (Northern Arizona University, Flagstaff, USA) found that intraspecific drought tolerance of pinyon pine was strongly associated with root-colonising ECM fungal species composition. Here, drought-tolerant pinyons tended to associate with *Geospora* spp., which increased water flow velocity in drought-tolerant seedling lineages and reduced it in intolerant lineages. A related study revealed that after successive droughts, ECM fungal species composition and abundance in roots of pinyon pines were responsive to tree mortality, with *Geospora* increasing and *Tuber* spp. decreasing in response to pine death (Mueller *et al.*, 2019). These studies indicate that the identity of mycorrhizal fungi and their interaction with certain host traits are critical for achieving restoration aims.

3. Advances in mycorrhizal research with sustainability applications

Understanding patterns of plant mycorrhizal type dominance, for instance in highly protected and valuable ecosystems, is key to understanding many ecosystem processes and their dynamics, and hence predicting limiting factors and environmental risks. In his keynote presentation, Richard Phillips (Indiana University, Bloomington, USA) presented a plethora of works describing differences in functioning between forests dominated by AM and ECM trees in similar climatic conditions (e.g. Zhang *et al.*, 2018). It had long been hypothesised that ECM-dominated forests accumulate more soil carbon, due in part to visibly greater production of recalcitrant organic matter. Yet when soils from ECM- and AM-dominated forests in proximity were compared to a depth of 1 m, greater accumulation of soil organic matter was found in AM-dominated forests (Craig *et al.*, 2018). Several talks presented at ICOM10 highlighted how processes such as C storage, soil enzymatic activities, nutrient cycling, and ecosystem-level sensitivity to global changes may vary (in part) because of mycorrhizal interactions (e.g. Haley Dunleavy Northern Arizona University, Flagstaff, USA; Tom Thirkell, University of Leeds, Leeds, UK; Melanie Jones, University of British Columbia, Kelowna, Canada). These results clearly stress the need to consider how the dominance of different mycorrhizal types may impact ecosystem function, and the consequences of host changes for broader ecosystem dynamics, management, and restoration. Nonetheless, subdominant plant species such as herbs and grasses in the forest understory can also play significant roles in ecosystems. For example, Rebecca Bunn (Western Washington University, Bellingham, USA) revisited the ‘direct mineral cycling hypothesis’ from the 1960’s and showed that AM fungal hyphae are active in forest leaf litter through cooperation with other microorganisms (e.g. Lin Zhang, China Agricultural University, Beijing, China), even in ecosystems dominated by ECM trees (Bunn *et al.* 2019). Despite these recent advances in using plant mycorrhizal type to investigate ecosystem processes, distinguishing between the plant mycorrhizal types (such as AM, ECM, or dual AM and ECM) is not always easily solved and different approaches coexist (Brundrett & Tedersoo, 2019; Bueno *et al.* 2019). ICOM10 facilitated an interesting debate in this respect, discussing possibilities for merging functional, morphological, and experimental approaches to tackle this important issue.

Studies of the functions of symbioses in the presence of their closest neighbours are also warranted. Marco Cosme (Université Catholique de Louvain, Louvain-la-Neuve, Belgium) illustrated the role that mycorrhizal fungi can play in ‘non-mycorrhizal’ plant functional responses, in which a presumed non-host species (*Arabidopsis thaliana*) in the presence of a mycorrhizal plant (*Medicago truncatula* colonised by the AM fungus *Rhizophagus* sp.)

exhibited root cortex colonisation. No nutrient exchange (via arbuscules) was observed, but the non-host plant exhibited activation of AM fungal-induced resistance to pathogens (Fernández *et al.*, 2019), indicating a functionally beneficial colonisation of the presumed non-host species. All in all, examining the multifunctional effects of the entire root mycobiome, including non-mycorrhizal and "fine root endophyte" fungi (Hoysted *et al.*, 2019) across plants, may be crucial to predicting the effect of global changes in natural and managed ecosystems.

4. Challenges

During the conference, key challenges facing mycorrhizal research (and researchers) in the coming decades were addressed:

Global change

Mycorrhizal symbioses are already highly complex, so how do we decipher mycorrhizal effects in systems subjected to multiple simultaneous pressures? Many speakers discussed mycorrhizal responses to climate change impacts such as drought, fire, and insect outbreaks (e.g. Philip Brailey, University of York, York, UK; Jean Carlos Rodríguez-Ramos, University of Alberta, Edmonton, Canada; Yong Zheng, Fujian Normal University, Fuzhou, China). Restoration of ecosystems exposed to pollutants (e.g. microplastics) was another common theme, as exemplified by Matthias Rillig (Freie Universität Berlin, Berlin, Germany)'s keynote talk. Species introductions of exotic fungi and/or exotic hosts are another important topic that potentially leads to fungal invasions. For example, global patterns in native vs introduced island floras revealed a strong tendency towards introduced mycorrhizal plants compared to non-mycorrhizal natives (Delavaux *et al.*, 2019), with some notable exceptions to the general pattern (e.g. Hawaii). Anne Pringle (University of Wisconsin-Madison, Madison, USA)'s research on *Amanita muscaria* (fly agaric) invasions in North America revealed that the population structure of this invasive fungus differed dramatically compared to its native range. The interactive effects of global change processes on mycorrhizal fungi and their hosts will undoubtedly provoke significant research effort from the mycorrhizal research community.

Methodological issues and advances

Although this topic is not new, finding ecologically relevant control for, and measurement of, the mycorrhizal status of plants is still controversial. Is "non-mycorrhizal" really an appropriate control condition for plants, given the prevalence of mycorrhizal fungi in natural and anthropogenic ecosystems (i.e., plants without mycorrhizal symbionts are rare), or would severing/restricting common mycorrhizal networks be more relevant experimental control (e.g. David Johnson, University of Manchester, Manchester, UK)?

The advent of modern high-throughput plant phenotyping systems has allowed us to begin characterising mycorrhizal host plant (shoot) growth responses (positive through to negative) over time (Watts-Williams *et al.*, 2019), rather than just at the harvest time point. This technology will be especially useful when it extends to root phenotyping platforms that allow for high resolution screening, and analysis of the effects of mycorrhizal fungi on root growth and morphology over time.

Several issues remain unresolved among the continual technological advances used for molecular work and interpretation of those data, as sequencing of mycorrhizal fungal communities becomes more commonplace. As Annegret Kohler (INRA, Nancy, France)'s keynote talk asked: What does gene copy number mean in terms of function? What does sequence abundance really mean in terms of species abundances? Many researchers uncritically present sequence abundances from NGS platforms as if they were equivalent to species relative abundances, although the ecological relevance of sequence abundance data needs to be cautiously addressed within the mycorrhizal (Nguyen *et al.*, 2015) and wider microbiome (Gloor *et al.*, 2017) research communities. Clearly, there needs to be more care with the use of metagenomic data and this may prove to be a suitable topic for a discussion session at a future ICOM.

Acknowledgements

This report is dedicated to the memory of the late Professor Sally E. Smith (1941 – 2019; https://nph.onlinelibrary.wiley.com/doi/full/10.1111/nph.15569). Sally's illustrious research career spanned more than 50 years and contributed important findings, particularly on the arbuscular mycorrhizal symbiosis. She inspired many young scientists to pursue careers in plant and mycorrhiza research, and she will be greatly missed by the mycorrhiza research community. Sally received the Eminent Mycorrhiza Researcher Award at ICOM10.

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Figure legends

Figure 1. ICOM10 covered a variety of recent basic and applied mycorrhizal research with a focus on topics that inform the sustainability of managed and natural ecosystems. Interactions between global change processes, and the interpretation of data from rapidly advancing sequencing technologies, emerged as common challenges for mycorrhizal researchers.

Figure 2. Planned and unplanned (in some cases unwanted) inputs into managed (e.g., agricultural, silvicultural) and natural mycorrhizal systems, and potential or existing outputs, which can extend to ecosystem and socio-economic impacts.

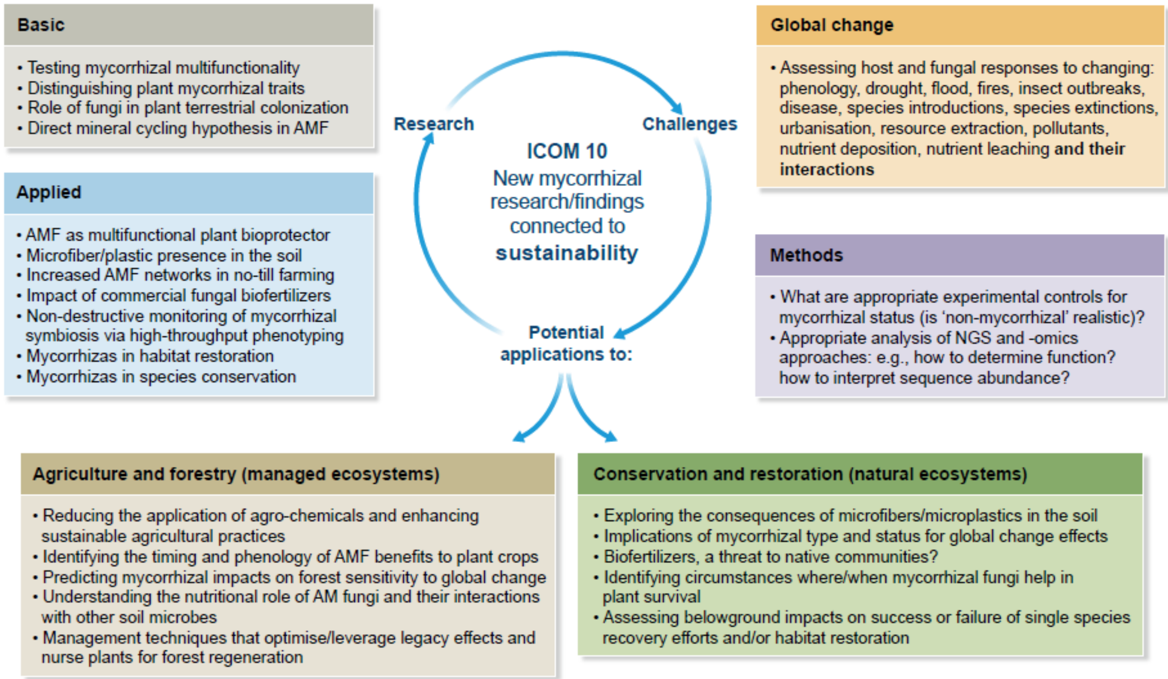
Basic
• Testing mycorrhizal multifunctionality
• Distinguishing plant mycorrhizal traits
• Role of fungi in plant terrestrial colonization
• Direct mineral cycling hypothesis in AMF
Applied
• AMF as multifunctional plant bioprotector
• Microfiber/plastic presence in the soil
• Increased AMF networks in no-till farming
• Impact of commercial fungal biofertilizers
• Non-destructive monitoring of mycorrhizal symbiosis via high-throughput phenotyping
• Mycorrhizas in habitat restoration
• Mycorrhizas in species conservation
Research
Challenges
ICOM 10
New mycorrhizal research/findings connected to
sustainability
Potential applications to:
Global change
• Assessing host and fungal responses to changing: phenology, drought, flood, fires, insect outbreaks, disease, species introductions, species extinctions, urbanisation, resource extraction, pollutants, nutrient deposition, nutrient leaching and their interactions
Methods
• What are appropriate experimental controls for mycorrhizal status (is 'non-mycorrhizal' realistic)?
• Appropriate analysis of NGS and -omics approaches: e.g., how to determine function? how to interpret sequence abundance?
Agriculture and forestry (managed ecosystems)
• Reducing the application of agro-chemicals and enhancing sustainable agricultural practices
• Identifying the timing and phenology of AMF benefits to plant crops
• Predicting mycorrhizal impacts on forest sensitivity to global change
• Understanding the nutritional role of AM fungi and their interactions with other soil microbes
• Management techniques that optimise/leverage legacy effects and nurse plants for forest regeneration
Conservation and restoration (natural ecosystems)
• Exploring the consequences of microfibers/microplastics in the soil
• Implications of mycorrhizal type and status for global change effects
• Biofertilizers, a threat to native communities?
• Identifying circumstances where/when mycorrhizal fungi help in plant survival
• Assessing belowground impacts on success or failure of single species recovery efforts and/or habitat restoration

Figure 1.

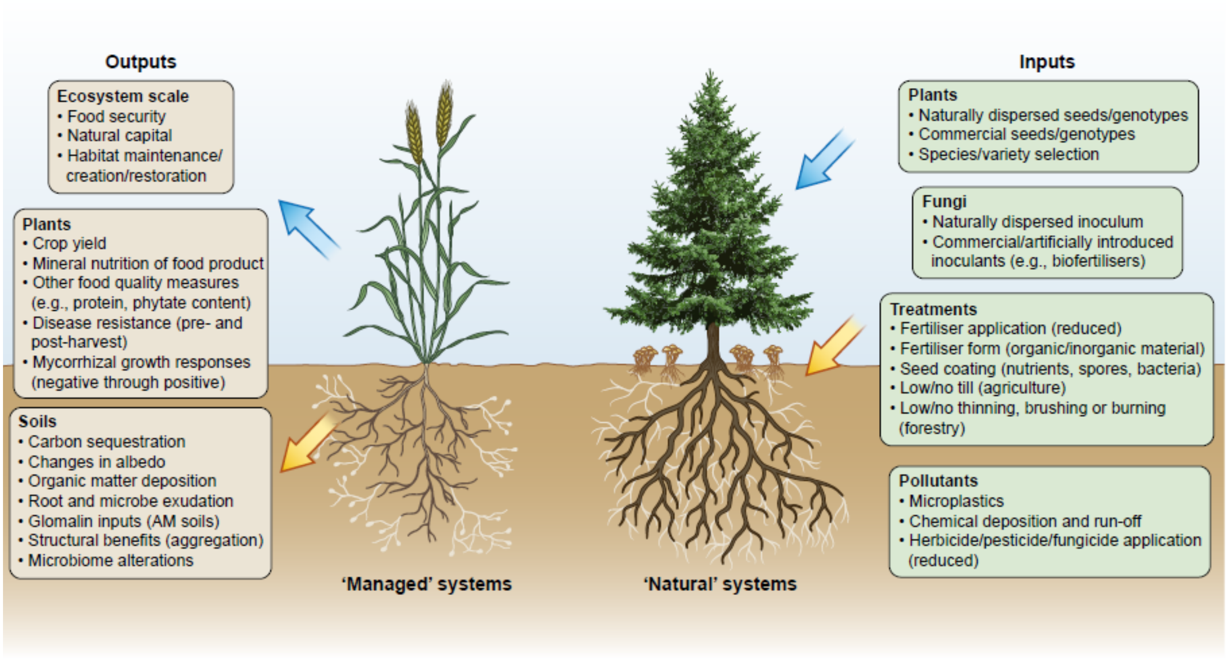
Outputs
Ecosystem scale
• Food security
• Natural capital
• Habitat maintenance/ creation/restoration
Plants
• Crop yield
• Mineral nutrition of food product
• Other food quality measures (e.g., protein, phytate content)
• Disease resistance (pre- and post-harvest)
• Mycorrhizal growth responses (negative through positive)
Soils
• Carbon sequestration
• Changes in albedo
• Organic matter deposition
• Root and microbe exudation
• Glomalin inputs (AM soils)
• Structural benefits (aggregation)
• Microbiome alterations
'Managed' systems
'Natural' systems
Inputs
Plants
• Naturally dispersed seeds/genotypes
• Commercial seeds/genotypes
• Species/variety selection
Fungi
• Naturally dispersed inoculum
• Commercial/artificially introduced inoculants (e.g., biofertilisers)
Treatments
• Fertiliser application (reduced)
• Fertiliser form (organic/inorganic material)
• Seed coating (nutrients, spores, bacteria)
• Low/no till (agriculture)
• Low/no thinning, brushing or burning (forestry)
Pollutants
• Microplastics
• Chemical deposition and run-off
• Herbicide/pesticide/fungicide application (reduced)

Figure 2.