



Mycorrhizae for a sustainable world

Article

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1 **Mycorrhizae for a sustainable world**
2 **The 10th International Conference on Mycorrhiza (ICOM10), Mérida, Mexico, June 30 –**
3 **July 5 2019**

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30 **Meeting report**

31
32 More than 80% of plant species exchange resources with mycorrhizal fungi and these
33 associations impact both partners at multiple scales, from individuals to ecosystems. 172
34 participants from 33 countries and 160 institutions met at the 10th International Conference on
35 Mycorrhiza in the city of Mérida in the Yucatan peninsula in Mexico – an area famous for its
36 Mayan archaeological sites, cenotes, and the Chicxulub impact crater that marks the end of the
37 Cretaceous period. They discussed latest advances on mycorrhizal research across 125 talks
38 and 111 posters in 14 sessions focused on the biology, physiology, ecology, evolution and
39 conservation of these interactions from molecules to biomes (Fig. 1). In particular, the
40 contribution of mycorrhizal research to sustainability in agriculture, conservation and
41 ecosystem restoration (Fig. 2) emerged as a promising topic to address today’s challenges in
42 the realm of human population growth, globalization and climate change.

43
44 **1. Sustainability in agriculture (managed ecosystems)**

45
46 Several speakers discussed the increasing abundance of commercial arbuscular mycorrhizal
47 products for agriculture, from “biofertilisers” to advances in seed coating technology (i.e.
48 adding mycorrhizal fungal spores directly to seeds along with nutrients and plant-helper
49 bacteria), and the interest in these products from growers.

50
51 A noticeable recurring theme was that commercial biofertilisers make rather dramatic claims
52 about their effectiveness, without evidence of their application leading to direct improvements
53 in crop yield or nutrition. Jan Jansa (Czech Academy of Sciences, Prague, Czech Rep.)’s
54 keynote presentation made the point that biofertilisers do not *create* nutrients per se; however,
55 they may help plants to access existing nutrient sources, and may provide non-nutritional
56 benefits. Examples of non-nutritional mycorrhizal benefits include increased soil glomalin
57 inputs, tolerance of microplastics inputs, and alteration of the soil microbiome (Svenningsen *et*
58 *al.*, 2018; de Souza Machado *et al.*, 2019; Hestrin *et al.*, 2019). Marcel van der Heijden
59 (Agroscope, Zurich, Switzerland) and Ashleigh Elliott (University of Leeds, Leeds, UK)
60 presented data on the application of commercial inoculants in field and glasshouse trials; crops
61 grown with a commercial arbuscular mycorrhizal (AM) fungal inoculant exhibited higher root
62 colonisation but there were few benefits to growth. Notably, the quality (in terms of active AM
63 fungal propagules) and effectiveness of different commercial products was highly variable.

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

72
73 In terms of alternative approaches to agriculture, Rillig & Lehmann (2019) identified
74 approximately 285,000 combinations of agricultural practices. In his keynote, Jan Jansa
75 emphasised the need to rigorously quantify the AM symbiosis and its effects in the field, to
76 enable the production of equations and models that make useful predictions, so that we can
77 best make use of the AM symbiosis as a valuable biological resource. Jansa also highlighted
78 the potential to look further down the production chain not only to crop productivity but to the
79 quality of the food product (e.g. do mycorrhizas affect food nutritional content, taste, or
80 spoilage), such as lowered pest impacts, postharvest disease reduction, and thus reduction of
81 food waste (e.g. AM fungi for food security).

82

83 **2. Sustainability in conservation and restoration (natural ecosystems)**

84

85 Effective use of the mycorrhizal symbiosis for restoration and conservation requires a deeper
86 understanding of mycorrhizal functionality and related ecosystem processes, and how these
87 processes and functions are altered through interactions with other actors and changing
88 conditions. For instance, several talks (e.g. Heike Bücking, South Dakota State University,
89 Brookings, USA; Ricardo Arraiano Castilho, Kew Gardens, London, UK) highlighted the
90 importance of local soil factors and host nutrient demand in shaping mycorrhizal fungal
91 communities, and whether changes in local environmental conditions associated with climate
92 change (i.e. drought) or nutrient deposition (i.e. soil fertility) may disrupt the structure of these
93 communities. Many speakers discussed the contribution of mycorrhizas in low impact,
94 sustainable approaches to ecosystem restoration (e.g. Brian Pickles, University of Reading,
95 Reading, UK; Cameron Egan, University of Hawai‘i, Mānoa, USA) and species conservation
96 (e.g. Nicole Hynson, University of Hawai‘i, Mānoa, USA; Louise Egerton-Warburton,
97 Chicago Botanic Garden, Glencoe, USA). Still, other mechanisms related to the activities of

98 mycorrhizal fungi, such as carbon sequestration (i.e. priming effect discussed by María Pozo,
99 EEZ-CSIC, Granada, Spain; and Johanna Pausch, University of Bayreuth, Bayreuth, Germany)
100 or the outcome of interactions among important actors, such as signaling pathways for kin
101 recognition (e.g. Monika Gorzelak, Agriculture and Agri-Food Canada, Lethbridge, Canada),
102 need to be accounted for when considering mycorrhizal applications in conservation and
103 ecosystem restoration.

104
105 A key theme is that different ecosystems may well need different approaches (i.e. there is no
106 “silver bullet” for restoration or conservation). For example, Louise Egerton-Warburton found
107 that “cedar” (*Widdringtonia wrighteii*) seedlings grew well in nursery conditions but
108 experienced drastic mortality following transfer to the field in Malawi. In turn, Nicole Hynson
109 and Cameron Egan’s work showed that incomplete recovery of Hawaiian native fungal
110 communities following successful growth of planted native host trees may compromise forest
111 restoration. However, the presence of diverse mycorrhizal fungal communities is not the only
112 requirement for a successful restoration plan. For instance, when comparing the performance of
113 AM fungal species on high- and low-quality (determined by associated fungal biomass) native
114 plant hosts in tallgrass prairie, Ylva Lekberg (MPG Ranch, Missoula, USA) found that AM
115 fungal identity and abundance influenced plant performance, while AM fungal species
116 diversity was unimportant in this regard. Similar results were found in a successional plant-
117 feedback study where only the appropriate late successional AM fungi with their corresponding
118 plant species grew faster and larger (Koziol & Bever, 2019). In the North American Southwest,
119 Catherine (Kitty) Gehring (Northern Arizona University, Flagstaff, USA) found that
120 intraspecific drought tolerance of pinyon pine was strongly associated with root-colonising
121 ECM fungal species composition. Here, drought-tolerant pinyons tended to associate with
122 *Geospora* spp., which increased water flow velocity in drought-tolerant seedling lineages and
123 reduced it in intolerant lineages. A related study revealed that after successive droughts, ECM
124 fungal species composition and abundance in roots of pinyon pines were responsive to tree
125 mortality, with *Geospora* increasing and *Tuber* spp. decreasing in response to pine death
126 (Mueller *et al.*, 2019). These studies indicate that the identity of mycorrhizal fungi and their
127 interaction with certain host traits are critical for achieving restoration aims.

128

129 **3. Advances in mycorrhizal research with sustainability applications**

130

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

159
160 Studies of the functions of symbioses in the presence of their closest neighbours are also
161 warranted. Marco Cosme (Université Catholique de Louvain, Louvain-la-Neuve, Belgium)
162 illustrated the role that mycorrhizal fungi can play in ‘non-mycorrhizal’ plant functional
163 responses, in which a presumed non-host species (*Arabidopsis thaliana*) in the presence of a
164 mycorrhizal plant (*Medicago truncatula* colonised by the AM fungus *Rhizophagus* sp.)

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

172

173 **4. Challenges**

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

176

177 *Global change*

178 Mycorrhizal symbioses are already highly complex, so how do we decipher mycorrhizal effects
179 in systems subjected to multiple simultaneous pressures? Many speakers discussed
180 mycorrhizal responses to climate change impacts such as drought, fire, and insect outbreaks
181 (e.g. Philip Brailey, University of York, York, UK; Jean Carlos Rodríguez-Ramos, University
182 of Alberta, Edmonton, Canada; Yong Zheng, Fujian Normal University, Fuzhou, China).

183 Restoration of ecosystems exposed to pollutants (e.g. microplastics) was another common
184 theme, as exemplified by Matthias Rillig (Freie Universität Berlin, Berlin, Germany)’s keynote
185 talk. Species introductions of exotic fungi and/or exotic hosts are another important topic that
186 potentially leads to fungal invasions. For example, global patterns in native vs introduced
187 island floras revealed a strong tendency towards introduced mycorrhizal plants compared to
188 non-mycorrhizal natives (Delavaux *et al.*, 2019), with some notable exceptions to the general
189 pattern (e.g. Hawaii). Anne Pringle (University of Wisconsin-Madison, Madison, USA)’s
190 research on *Amanita muscaria* (fly agaric) invasions in North America revealed that the
191 population structure of this invasive fungus differed dramatically compared to its native range.
192 The interactive effects of global change processes on mycorrhizal fungi and their hosts will
193 undoubtedly provoke significant research effort from the mycorrhizal research community.

194

195 *Methodological issues and advances*

196 Although this topic is not new, finding ecologically relevant control for, and measurement of,
197 the mycorrhizal status of plants is still controversial. Is “non-mycorrhizal” really an appropriate
198 control condition for plants, given the prevalence of mycorrhizal fungi in natural and

199 anthropogenic ecosystems (i.e., plants without mycorrhizal symbionts are rare), or would
200 severing/restricting common mycorrhizal networks be more relevant experimental control (e.g.
201 David Johnson, University of Manchester, Manchester, UK)?

202
203 The advent of modern high-throughput plant phenotyping systems has allowed us to begin
204 characterising mycorrhizal host plant (shoot) growth responses (positive through to negative)
205 over time (Watts-Williams *et al.*, 2019), rather than just at the harvest time point. This
206 technology will be especially useful when it extends to root phenotyping platforms that allow
207 for high resolution screening, and analysis of the effects of mycorrhizal fungi on root growth
208 and morphology over time.

209
210 Several issues remain unresolved among the continual technological advances used for
211 molecular work and interpretation of those data, as sequencing of mycorrhizal fungal
212 communities becomes more commonplace. As Annegret Kohler (INRA, Nancy, France)'s
213 keynote talk asked: What does gene copy number mean in terms of function? What does
214 sequence abundance really mean in terms of species abundances? Many researchers
215 uncritically present sequence abundances from NGS platforms as if they were equivalent to
216 species relative abundances, although the ecological relevance of sequence abundance data
217 needs to be cautiously addressed within the mycorrhizal (Nguyen *et al.*, 2015) and wider
218 microbiome (Gloor *et al.*, 2017) research communities. Clearly, there needs to be more care
219 with the use of metagenomic data and this may prove to be a suitable topic for a discussion
220 session at a future ICOM.

221

222 **Acknowledgements**

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

229

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235

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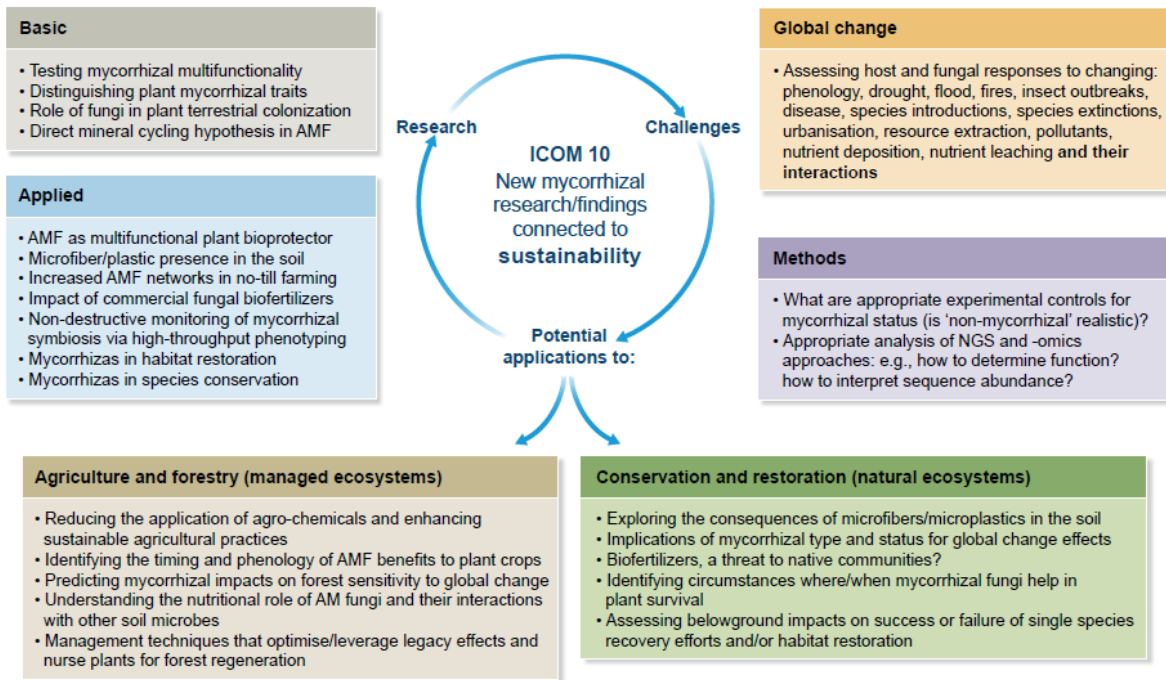
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- 286

287 **Figure legends**

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

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

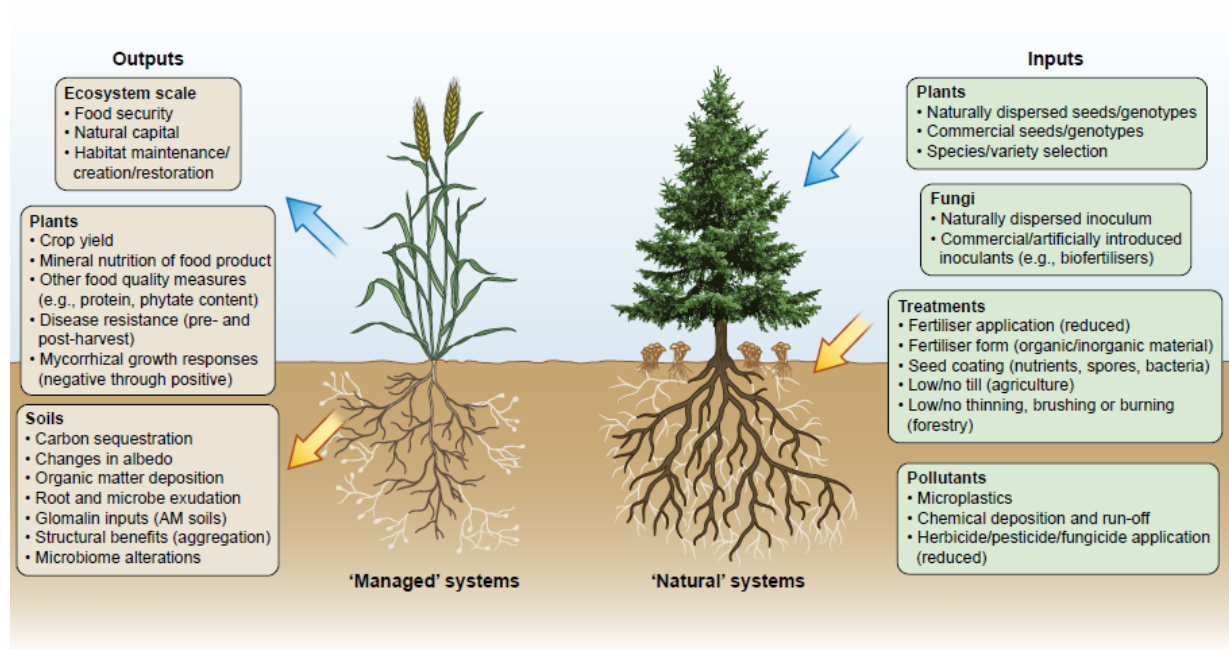
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296

297 **Figure 1.**

298



299

300 **Figure 2.**