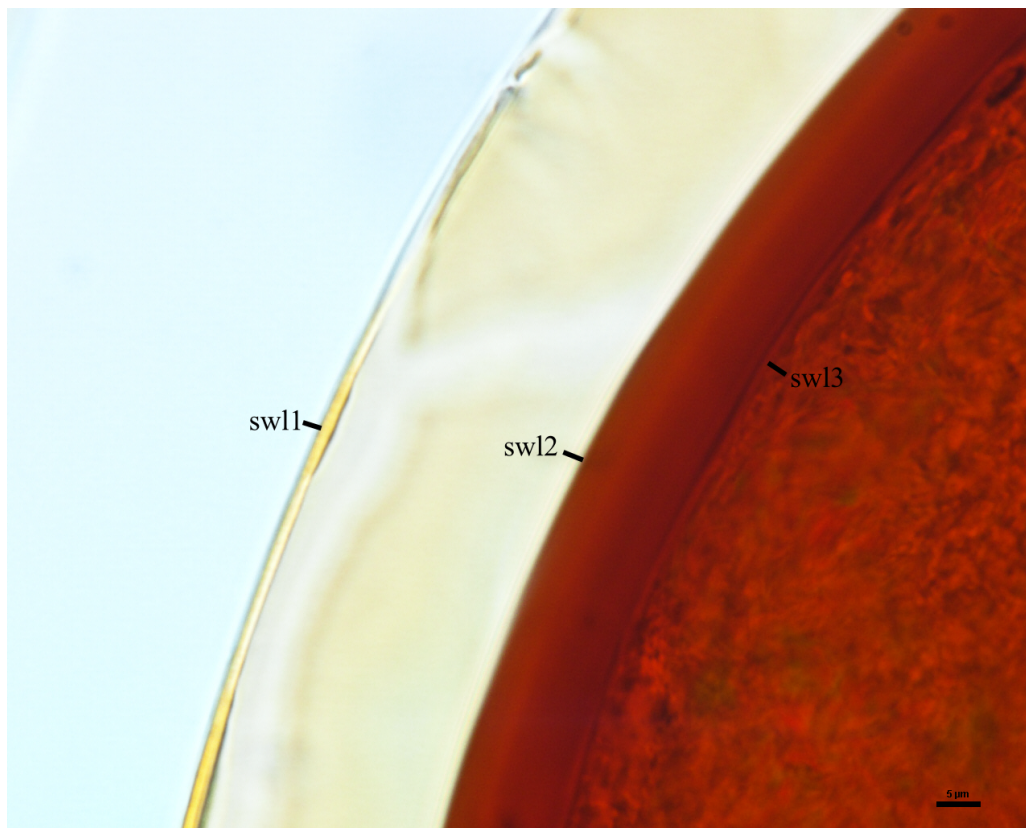




# IMS Newsletter

*The International Mycorrhiza Society quarterly e-newsletter*



***Gigaspora* sp.**

By: Dr. Bruno Tomio Goto, Universidade Federal do Rio Grande do Norte, Brazil.

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## Editor-in-Chief

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*Evolution* – Jason Hoeksema, University of Mississippi, US  
*Molecular biology* – Jonathan Plett, Western Sydney University, Australia  
*Applications* – Pedro M. Antunes, Algoma University, Canada

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# 11th Editorial of the International Mycorrhiza Society Newsletter

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This is the 11<sup>th</sup> issue of the International Mycorrhiza Society Newsletter. It appears just before the III International Symposium of the Mycorrhizal Symbiosis in South America (<https://southmycorrhizas.org/events/>), and after important mycological and ecological meetings like the Mycological Society of America, Latin American Mycology Conference, and Ecological Society of America, some of which, we will report soon. We keep encouraging worldwide mycorrhizal researchers in all stages to share their research outputs and/or ideas with us (in a short article or YouTube interview way).

## In this issue...

The Top 10 mycorrhizal research papers of the last four months (papers published between January and April 2023), include a *Commun Biol* article by Marco Cosme (as sole author) (Rank 1). He used a phylogenetic comparative method and showed that mycorrhizas drive the evolution of plant adaptation to drought. The second-best paper was by, Maillard *et al.* (*New Phytol*) combining isotopic, genomic, and transcriptomic methods to elucidate the degradation of chitin by ectomycorrhizal fungi. They found a significant relationship between the capacity of ectomycorrhizal fungi to assimilate organic

nitrogen from chitin and their genomic and transcriptomic potentials for chitin degradation. The third rank was for a paper by Karst *et al.* performing a meta-analysis (*Nat Ecol Evol*) critically analyzing three common claims on common mycorrhizal networks (CMNs) in forests: namely that CMNs are common, that they allow sharing resources among trees, and mature trees and communicate with offspring through CMNs. Their analysis was based on a thorough literature review and raised considerable discussion among scientists and in the media.

This 11<sup>th</sup> IMS Newsletter issue includes four short articles. The first one, by César Marín (Universidad Santo Tomás), is entitled “Paradigm shifts and recent mycorrhizal 'controversies'”. In this article three different 'controversies' in mycorrhizal ecology are discussed: the existence and/or functionality of CMNs, how to define mycorrhizal traits, and the use of AM-based biofertilizers. The second article is by, by Matthias J. Salomon (University of Adelaide) on the current state and pathways of AM fungal inoculants and that many commercial products do not contain viable mycorrhizal fungi. Related to this, Vasilis Kokkoris (Vrije Universiteit Amsterdam) and Nicolas Corradi (University of

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Ottawa) wrote about how our increasing understanding of the complex AM fungal genetics could affect the application of bio-fertilizers. A fourth article by Liz Koziol and co-authors at the University of Kansas relates the story of the International Culture Collection of (Vesicular) Arbuscular Mycorrhizal Fungi (INVAM) and its current move to that University.

Finally, in addition to our traditional Tools and Events sections (with quite several mycological and mycorrhizal events coming up in the next few years), please find YouTube interviews with Katie Field about the first evidence that fine root endophytes (phylum Mucoromycotina) are nutritional mutualists with a flowering plant, and to Laura van Galen about correlated evolution in an ectomycorrhizal host (*Nothofagus*) - symbiont system across New Zealand. Please enjoy this newsletter and we also look forward to feedback, recommendations, or short articles for the next newsletters.



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# Top 10 papers on mycorrhizal research\*

1. Cosme M. 2023. Mycorrhizas drive the evolution of plant adaptation to drought. *Commun Biol* 6:346. <https://doi.org/10.1038/s42003-023-04722-4>
2. Maillard F, Kohler A, Morin E, *et al.* 2023. Functional genomics gives new insights into the ectomycorrhizal degradation of chitin. *New Phytol* 238:845-858. <https://doi.org/10.1111/nph.18773>
3. Karst J, Jones MD, Hoeksema JD. 2023. Positive citation bias and overinterpreted results lead to misinformation on common mycorrhizal networks in forests. *Nat Ecol Evol* 7:501-511. <https://doi.org/10.1038/s41559-023-01986-1>
4. Jörgensen K, Clemmensen KE, Wallander H, Lindahl BD. 2023. Do ectomycorrhizal exploration types reflect mycelial foraging strategies?. *New Phytol* 237:576-584. <https://doi.org/10.1111/nph.18566>
5. Wang L, Zhang L, George TS, Feng G. 2023. A core microbiome in the hyphosphere of arbuscular mycorrhizal fungi has functional significance in organic phosphorus mineralization. *New Phytol* 238:859-873. <https://doi.org/10.1111/nph.18642>
6. Van Nuland ME, Ke PJ, Wan J, Peay KG. 2023. Mycorrhizal nutrient acquisition strategies shape tree competition and coexistence dynamics. *J Ecol* 111:564-577. <https://doi.org/10.1111/1365-2745.14040>
7. Thomas PW, Jump AS. 2023. Edible fungi crops through mycoforestry, potential for carbon negative food production and mitigation of food and forestry conflicts. *Proc Natl Acad Sci USA* 120:e2220079120. <https://doi.org/10.1073/pnas.2220079120>
8. Shemesh H, Bruns TD, Peay KG, Kennedy PG, Nguyen NH. 2023. Changing balance between dormancy and mortality determines the trajectory of ectomycorrhizal fungal spore longevity over a 15-yr burial experiment. *New Phytol* 238:11-15. <https://doi.org/10.1111/nph.18677>
9. Deng M, Hu S, Guo L, *et al.* 2023. Tree mycorrhizal association types control biodiversity-productivity relationship in a subtropical forest. *Sci Adv* 9:eadd4468. <https://doi.org/10.1126/sciadv.add4468>
10. Formenti L, Ahlstrand NI, Hassemer G, *et al.* 2023. Macroevolutionary decline in mycorrhizal colonization and chemical defense responsiveness to mycorrhization. *iScience* 26:106632. <https://doi.org/10.1016/j.isci.2023.106632>

\*Selected from 174 Web of Science articles published between *January – April*, 2023 by: Justine Karst, Jonathan Plett, Jan Jansa, Jason Hoeksema, Judith Lundberg-Felten, Bala Chaudhary, Annegret Kohler, Joseph Cooper, Junling Zhang, and César Marín.



# Research commentaries

## Paradigm shifts and recent mycorrhizal 'controversies'

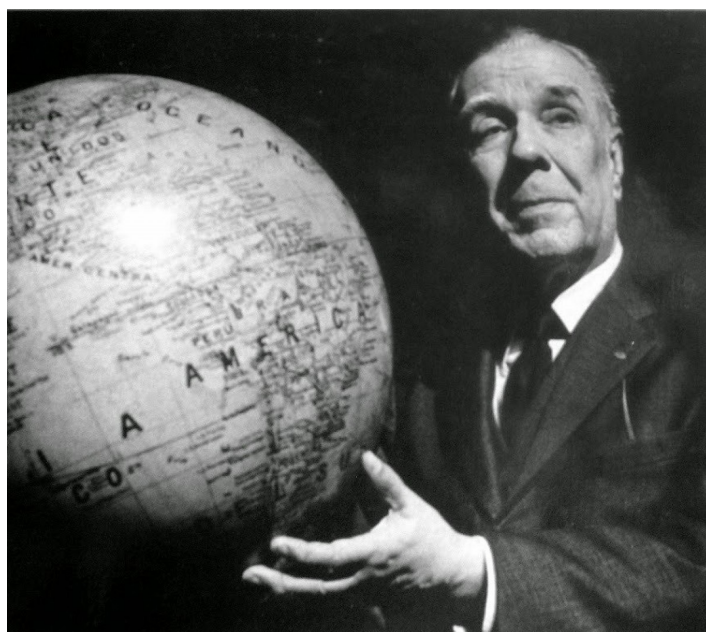
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In his short story “*On Exactitude in Science*” (Borges 1998), Jorge Luis Borges compared the scientific endeavor to that of cartographers creating a map of an Empire. The cartographers created a map as big as the Empire itself, which ended up being useless. Models and scientific theories follow this logic and constitute approximations to reality – because an extremely detailed model ends up being useless, and as such, some degree of uncertainty is expected. Thus, as a map, scientific theories sometimes omit or summarize some information. The logical consequence of this is that paradigm shifts are expected (Kuhn 1962; Okasha 2016) – as each shift might represent an even closer approximation to 'reality'. Mycorrhizal research –particularly mycorrhizal ecology and evolution- is not exempt of such shifts, which cause significant controversy (Albornoz *et al.* 2021). In particular, in recent years, three important debates have developed in mycorrhizal research: 1. On misinformation regarding common mycorrhizal networks in forests . 2. On the definition of mycorrhizal types. 3. On the effectiveness of bio-fertilizers based on arbuscular mycorrhizal (AM) fungi.

### **Misinformation on common mycorrhizal networks in forests**

One of the most popularized mycorrhizal concepts that the general public is familiar with are the so



**Jorge Luis Borges.** Photo from: Eterna Cadencia.

called 'common mycorrhizal network' (CMN). A CMNs are “are physical, continuous linkages among the roots of at least two different individual plants, by the same genetic individual of mycorrhizal fungus” (Karst *et al.* 2023). A well known example of CMNs is given by mycoheterotrophic plants, which acquire carbon from mycorrhizal fungi that colonizes other plants (Merckx and Freudenstein 2010). But most of the focus on popular media regarding CMN has been in forests, particularly in the notion of 'Mother trees' able to communicate and share resources with seedlings through a CMN. Dozens of science outreach books, videos, movies, and other types of media have shared this notion, particularly

since journalists at *Nature* deemed CMNs as the 'wood wide web' (and in their cover), based on a seminal paper by Simard *et al.* (1997) on the same journal issue.

Recently, though, Karst *et al.* (2023) have questioned three common claims regarding CMNs. First, that CMNs are present in all forests: after reviewing the literature, they found that just two tree (out of 73,300 global tree species; Cazzolla Gatti *et al.* 2022) and three ectomycorrhizal (ECM) fungal species have been genotypically mapped around the globe (in Canada and Japan). The hyphae of these shared fungal genets could easily break and does not prove nutrient transfer. A second common claim is that nutrients/resources are transferred through CMNs, which increases plant growth. After reviewing hundreds of papers, the authors got 18 highly cited studies and examined how those citations made supported or unsupported claims on the original research (Karst *et al.* 2023). These studies were directly performed in forests, *in situ* – the authors also comment about laboratory studies. Karst *et al.* (2023) identify alternative explanations for such positive effects: i. Part of the resource transfer pathway is discontinuous, involving the flow of solutes in the soil solution (and not necessarily in the CMN); ii. Fungal pathogen composition was altered due to experimental treatment (ie. when seedlings are grown in containers) which alters seedling performance; iii. Similarly, the mycorrhizal composition changed due to the treatments; iv. Access to surrounding roots positively influences seedling performance; and iv. The treatment reduced the soil volume for fungal foraging, affecting the non-CMN seedlings. Thus, it seems, the CMN experiments conducted so far do not exclude such alternative explanations which are consistent with the complexity of soil ecology. A third common claim is that mature trees

communicate with offspring through CMNs, for which Karst *et al.* (2023) found no evidence at all.

Other recent articles have also questioned how common (or not) are CMNs (Figueiredo *et al.* 2021; Henriksson *et al.* 2023; Kuyper and Jansa 2023). Regarding this, Henriksson *et al.* (2023) inquired three aspects: ectomycorrhizal Carbon metabolism, patterns of (ectomycorrhizal) trees forest regeneration, and the CMN studies using isotopic methods. They conclude that there is evidence for C movement among plants but the role of CMNs is not clear, neither that CMNs provide growth benefits. Also, so far, we do not know any physiological mechanism allowing C fluxes from ECM fungi into the plant–fungal interface (Henriksson *et al.* 2023). Also, forest regeneration patterns in boreal forests are not congruent with what would be expected if they were connected through CMNs (Henriksson *et al.* 2023).

What this very relevant and on point criticism towards the CMN literature should cause is an improvement in experimental settings and controls *in vivo* and *in vitro*. Karst *et al.* (2023) propose some of these experimental design improvements. Some journals, like *Functional Ecology* have recently made a special issue call around mycorrhizal networks with this consideration. Still, some observations are thought-provoking. For example, it has been observed that seedlings growing together with larger, mycorrhized plants grew larger than seedlings growing with larger, non-mycorrhized plants (van der Heijden and Horton 2009) – in at least half of experiments. Processes other than CMNs could explain this, like the transfer of N and P, indirect effects (ie. being close to a fungus associated to a 'healthy' tree), or hyphospheres (Wang *et al.* 2023; Johnson and Marín 2023) might explain such patterns. Definitely more

research is needed, considered all possible explanations. Also, anastomosis and hyphal healing mechanisms are quite common in arbuscular mycorrhizal fungi (de la Providencia et al. 2004; Purin and Morton 2013), which do not imply the functionality per sé of a CMN, but its existence is at least very interesting.



*Die Sprache der Pilze (Biosemiotik I)*. By: Heiko Sievers. watercolor and pencil on paper, h 32 x w 24 cm, 2023  
<http://mushroom-of-the-day.blogspot.com/>

### Different approaches to define and diagnose mycorrhizal types

Symbiotic associations between plant and mycorrhizal fungi mediate plant populations and community diversity and ultimately impact global biogeochemical cycles and ecosystem services (Tedersoo et al. 2020). Different types of mycorrhizal associations exist including ectomycorrhizas (ECM), arbuscular mycorrhizas

(AM), orchid mycorrhizas (OM) and ericoid mycorrhizas (ERM) (Moora 2014), which are broadly related to different nutrient economies (Phillips et al. 2013). It is important to identify and diagnose mycorrhizal types of vascular plants at all scales -from local to global, in order to identify effects of mycorrhizas in ecosystems. Furthermore, mapping global mycorrhizal types has been a priority in mycorrhizal ecology over the last three decades (Read 1991; Steidinger et al. 2019; Tedersoo et al. 2022).

In order to accomplish such global mapping efforts, it is necessary to know the mycorrhizal types of the global vascular flora. Bueno et al. (2019a) identified two approaches to assign mycorrhizal traits of plant species: the empirical approach and the taxonomic approach. The information source for the former is “published empirical studies describing plant root mycorrhizal associations”, while “researcher expertise is used for extrapolating either mycorrhizal type or status to complete taxonomic groups, such as genus or family, based on background empirical information from one or a few species from the same group” for the latter (Bueno et al. 2019a). Both approaches have important assumptions: the empirical approach assumes that the accumulated empirical data are correct, while the taxonomic approach assumes that mycorrhizal traits are completely conserved at the chosen taxonomic level (Bueno et al. 2019a). A highly cited paper regarding the proportions of mycorrhizal types associated with global flora uses the taxonomic approach (Brundrett and Tedersoo 2018). Using such expertise-based generalizations has caused significant controversy (Bueno et al. 2019a; Sun et al. 2019).

Such debate and the above-mentioned assumptions have led to some interesting developments. In particular, Brundrett and



Tedersoo (2019) have argued that a significant portion of the mycorrhizal literature contains 'mycorrhizal trait allocation errors' (Brundrett 2021) because root mycorrhizal structures have been incorrectly identified, and because such 'incorrect' diagnoses have been recycled many times in the citing literature.

Instead, they propose a specific set of criteria for diagnosing each mycorrhizal type and checking the mycorrhizal literature (and databases) against their curated list (Brundrett and Tedersoo 2018). As a response, Bueno *et al.* (2019b) ask the following questions: Should only the presence of arbuscules define AM plants? Can plant taxonomy be a reliable predictor of plant mycorrhizal traits? Should the results of published studies be considered 'incorrect' when they do not match any proposed 'standard reference'?

Ultimately, this debate raises important questions about what a mycorrhiza is. For example, Bueno *et al.* (2020) argues that in the *FungalRoot* database introduction (Soudzilovskaia *et al.* 2020), by proposing the only use of the 'arbuscule criterion' to assign a plant as AM, it is excluding the many (and highly understudied) non-nutritional functions that AM fungi perform (Delavaux *et al.* 2017), which could be expressed by the presence of arbuscular intraradical hyphae. This focus on nutritional exchange also seems to 'forget' that AM symbioses work in a mutualism-to-parasitism continuum (Johnson *et al.* 1997) and some AM fungi do not form arbuscules (e.g. ancient AMF families) (Redecker *et al.* 2013). Important issues regarding the definition of 'AM-facultivate' plants have also arise during this debate (Bueno *et al.* 2020; Soudzilovskaia *et al.* 2022) – recently, other authors have criticized the usefulness of this term at all (Kuyper and Jansa 2023).

I invite our readers to read all the cited literature here, to build their own opinions. Independently of the position taken, from the point of view of the development of mycorrhizal research, it is interesting to see how the need to establish global mapping efforts and global databases on mycorrhizal traits, has led to go back to the fundamental biology, ecology, functionality, and most importantly, definition of the mycorrhizal symbioses.

### **Effectiveness of bio-fertilizers based on AM fungi**

Short articles by Matthias J. Salomon (Pag. 10) and by Vasilis Kokkoris and Nicolas Corradi (Pag. 13) in this issue discuss about the effectiveness of AM fungi as bio-fertilisers. In short, although over the last two or three decades there has been a lot of interest of using AM fungi as biofertilizers, just recently Salomon *et al.* (2022a) thoroughly evaluated 25 commercial inoculants containing AM fungi. They found that only 5 inoculants had viable propagules and a significant mycorrhizal root colonization (Salomon *et al.* 2022a). In addition, many AM-based biofertilizers do not contain the declared AM fungal species, as revealed by metabarcoding sequencing (Vahter *et al.* 2023). Given this, a general framework and criteria for AM fungal inoculants was established (Salomon *et al.* 2022b). Such criteria include: plant bio-assays to verify that the AM fungi have colonize plant roots, verify inoculum composition and its viability, avoid negative effects of the carrier material, and detailed labeling. Some companies do abide to such criteria in addition to use native consortia inoculum (4-5 species from different genera) and follow the inoculated crop soil ecology (Aguilera *et al.* 2023).

### **Acknowledgments**

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## Current state and future pathways of arbuscular mycorrhizal inoculants

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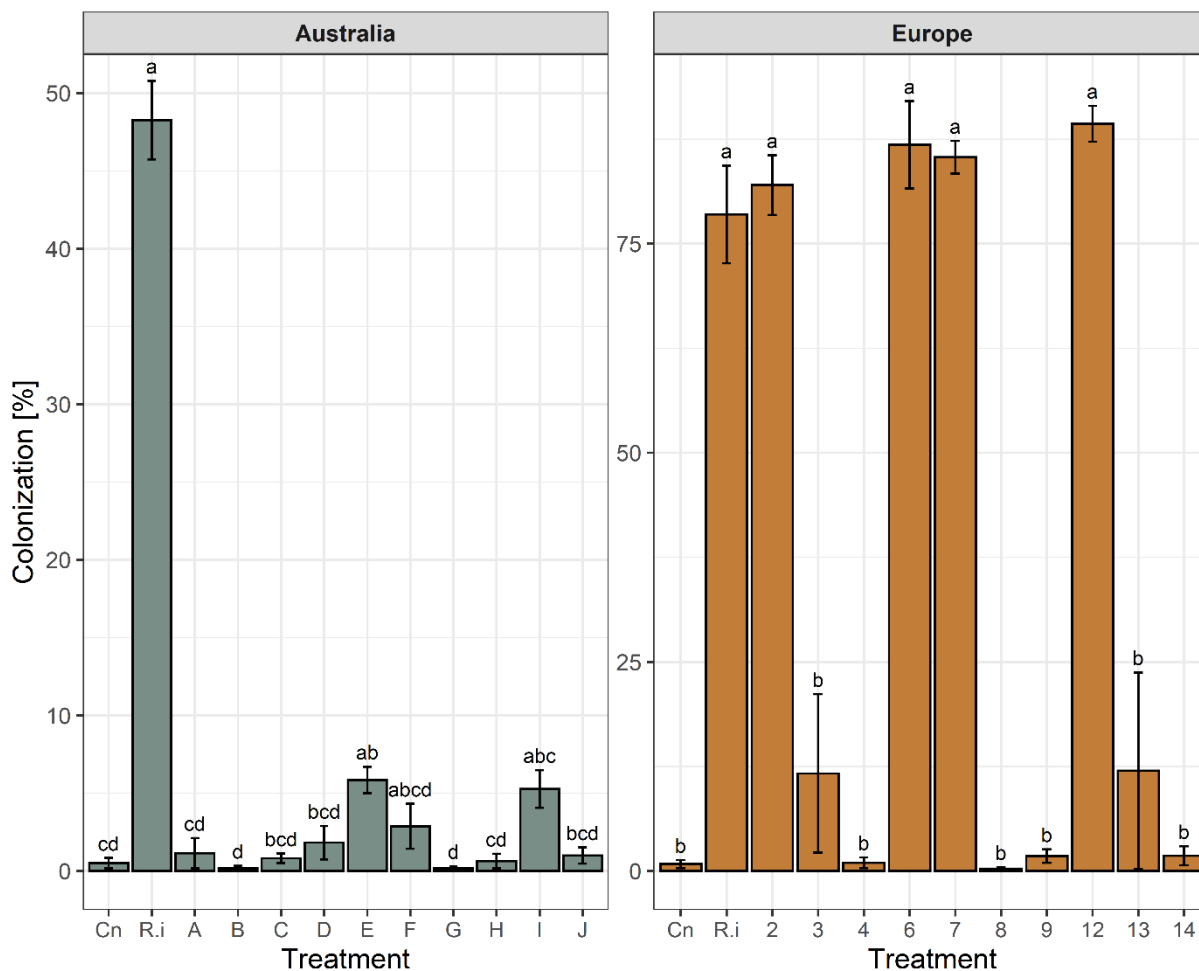
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In recent years, there has been a growing interest in the application of arbuscular mycorrhizal (AM) inoculants to improve plant health and productivity. Commercial inoculants are available in various forms, including granules, powders and liquids, and are promoted to both professional and amateur growers. With an increasing market capitalisation of beneficial plant growth promoting microorganisms, questions remain about the quality of commercial products and whether they provide any benefit to plants or soils.

A recent study published in the journal *Appl Soil Ecol* evaluated the effectiveness of commercial mycorrhizal inoculants in a global setting (Salomon *et al.* 2022a). While there have been previous studies in this area, this particular study stands out due to its extensive coverage and global perspective. The study rigorously tested 25 commercial inoculants containing arbuscular mycorrhizal fungi (AMF) in a greenhouse environment, measuring their viability and influence on plant growth under controlled conditions. This greenhouse study was carried out in Australia and Europe, with 10 and 15 inoculants being tested at each location, respectively. The selection criteria for these products required them to be commercially available and to contain AMF propagules. Additionally, three selected inoculants, proven effective in inducing arbuscular mycorrhizal root colonization, were evaluated under field conditions in a North-American study to determine their impact on the native mycorrhizal community. The

study's results were somewhat disconcerting: only 5 out of the 25 tested inoculants contained viable propagules in the greenhouse experiments, leading to mycorrhizal root colonization under AMF-favorable conditions (Fig. 1). Significant growth benefits were observed when compared against plants in a sterile control environment, but these benefits diminished when tested in non-sterilized (real world) soil, which contains a natural microbial community. Under these conditions, only one product exhibited a significant increase in biomass relative to the control treatment. The field study indicated that mycorrhizal growth effects weren't associated with the percentage of mycorrhizal root length colonized but were instead tied to a shift in the AMF community, displacing indigenous species. Only one AMF inoculant resulted in a significantly higher biomass. Nonetheless, the authors intentionally avoid offering specific details about the inoculants to prevent the identification of any particular product.

This study underscores the need for stringent quality control measures in order to establish efficient commercial AMF inoculants as the norm rather than the exception. This could be achieved through government regulatory bodies or voluntary quality control certificates of AM inoculant producers. However, any method of assessing AMF viability and effectiveness must strike a balance between economic costs and practical significance. Recently, the authors of the aforementioned study, along with other experts



**Figure 1.** Mycorrhizal root colonization in the Australian and European study of the global evaluation of commercial arbuscular mycorrhizal inoculants. Significant root colonization found in the positive control treatments of both studies using *Rhizophagus irregularis* (R.i.) and treatments 2, 6, 7, and 12 of the European study. From Salomon *et al.* (2022a).

within the mycorrhizal community proposed minimum quality criteria and suggested a standardized bioassay to verify the effectiveness of AM inoculants (Salomon *et al.* 2022b). The paper also called for more research and although the scope of research questions appears boundless, it is imperative that the safety of the widespread use of AM inoculants takes precedence. Subsequent research should then pivot to economic considerations, such as the cost-effective production of AMF inoculum and the identification of isolates that yield predictable plant growth outcomes.

After decades of research, the widespread use of AMF inoculum in agriculture or nature restoration

of compromised systems still seems a long way off. However, we have also seen fantastic research progress in recent years, such as the advances in *in vitro* propagation of sterile inoculum (Tanaka *et al.* 2022). The global evaluation of commercial AM inoculants revealed that most products lacked viable propagules, yet it's crucial to note that a handful of products met all the criteria for inoculum reliability or viable spore count. While the mycorrhizal growth effect remains somewhat unpredictable when introduced to non-sterilized soil on greenhouses or under field conditions, this research also indicates that plant growth benefits are probable when these inoculants are applied to soils with low natural microbial diversity and abundance. Drawing from the evidence currently

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available, commercial AM inoculants can be effective under specific scenarios, such as in horticulture when working with pasteurized substrates, or in natural soils where the natural microbial community has been reduced due to various factors

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## AMF genetics and the future of AMF applications

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One widely implemented approach to promote agricultural sustainability involves harnessing the beneficial properties of the soil microbiome via the application of bio-fertilizers (Gianinazzi and Vosatka 2004). These products are employed to enhance yield and safeguard plants against various environmental stressors. Among the most notable microbial candidates for bio-fertilizer applications, are the arbuscular mycorrhizal fungi (AMF) (Berruti *et al.* 2016). Remarkably, a single AMF species can simultaneously colonize multiple mycorrhizal plant species and, similarly, a single plant can also be colonized by multiple AMF individuals. Together, these mechanisms can significantly foster extensive underground hyphal networks. These enhance nutrient uptake, including phosphate and nitrate, as well as improve water absorption for the plants (Giovannetti 2008; Garg and Chandel 2010). Moreover, AMF can provide protection against pathogens, and various abiotic stresses such as salinity and drought (van der Heijden *et al.* 2015), offering resilience in the face of environmental challenges (Marro *et al.* 2022). In return, plants supply AMF with photosynthetically-derived carbon in the form of lipids, which are crucial for their growth and survival (Rich *et al.* 2017).

With approximately 345 described species, the taxonomic diversity of AMF seems surprisingly limited (Redecker *et al.* 2013). In contrast, recent phylogenetic assessments based on genome data, revealed very high genome diversity in the model species *Rhizophagus irregularis* (Savary *et al.*

2018; Sperschneider *et al.* 2023), overall suggesting that the number of AMF species may have been severely underestimated. In any case, currently defined AMF species possess the ability to interact with a wide range of mycorrhizal plant hosts, leading to their classification as generalists (Smith and Read 2008). Despite their generalist nature, significant functional variation exists both between (Klironomos 2003) and within (Munkvold *et al.* 2004; Koch *et al.* 2006) AMF species. Specifically, a single AMF species can comprise hundreds of functionally distinct strains, each with unique genome characteristics, which highlights the presence of substantial intraspecific and interspecific functional and molecular diversity (Kokkoris and Hart 2019a; Kokkoris *et al.* 2021). This significant variation challenges the notion that all AMF are equally effective and beneficial to their hosts - evidence that is unfortunately often ignored in the marketing strategies of companies selling AMF-based inocula. Compelling evidence now indicates that this variability correlates with significant differences in genetics and epigenetics both among and within AMF species (Ropars *et al.* 2016; Chen *et al.* 2018a; Sperschneider *et al.* 2023).

### Current state of AMF based biofertilizers

Currently, most AMF bio-fertilizers rely heavily on a single species and particularly on the homokaryotic strain, *Rhizophagus irregularis* DAOM 197198 (Basiru *et al.* 2020). This strain has gained popularity due to its rapid growth, ease of manipulation and propagation in

laboratory settings, and high spore production (Ceballos *et al.* 2013; Rosikiewicz *et al.* 2017). Overall, these traits create the impression that DAOM-197198 is highly beneficial for plant growth. However, previous studies have revealed that the standard laboratory propagation conditions and the strain's prolific sporulation ability can also result in reduced nutritional benefits for the host plants (Kokkoris and Hart 2019a, b; Kokkoris *et al.* 2019a). Ironically, under stressful environmental conditions, this strain has even been shown as causing detrimental effects on the nutritional status of the host plants, possibly by “selfishly” hoarding nutrients (Kokkoris *et al.* 2019b). This raises concerns about the efficacy of such products and especially when applied under stressful environmental conditions, such as in saline soils, or dry fields, as well as the environmental safety of this practice in terms of its impact on the broader soil ecosystem (Thomsen and Hart 2018; Cornell *et al.* 2021).

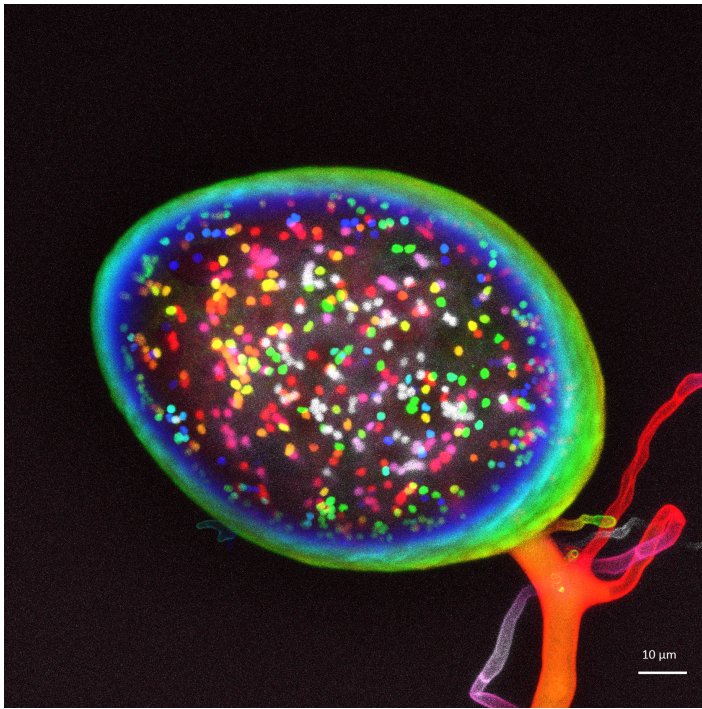
Overall, the disparity between local farming conditions, strain origin, and inoculum propagation conditions can also lead to unsuccessful inoculations. For example, the introduced inoculum might fail to establish (Farmer *et al.* 2007; Thomsen *et al.* 2021) or to provide any benefits to the intended crops (Hamel and Smith 1991; Ryan and Graham 2002; Kokkoris *et al.* 2019c). In its quest for a universally applicable product, the inoculum industry tends to neglect the essential functional aspects of AMF. In particular, it overlooks the role of (epi)genetic and functional variation that dictates strain specificity and may help with the process of adaptability to environmental change. While adaptability to specific environments plays a critical role in the success of inoculation efforts, here we will discuss the significance of functional variation resulting from genetic diversity, considering the rapid advancements in the field.

## High AMF genome diversity and inoculum production

In recent years, advances in sequencing technologies have facilitated a better acquisition of genome data from AMF. This led to significant improvements in the understanding of genetic and epigenetic organization of these fungi, and their potential downstream effects on functional diversity. This link is particularly true for the model species *R. irregularis*, which has been shown to carry significant intraspecific (within species) genomic diversity and differences in nuclear organization. The presence of high genetic differences among *R. irregularis* strains, including those harvested from the same field (Koch *et al.* 2004; Corradi *et al.* 2007), has been known for some time, but recent genome sequencing explorations have finally uncovered the basis of this variation. Specifically, genome analyses show that isolates proposed to belong to *R. irregularis* carry wildly different genomes, varying in some cases up to 50% in gene content (Chen *et al.* 2018a; Yildirim *et al.* 2022). Recent chromosome-level assemblies confirmed this, but also uncovered variation in chromosome structure and size. Epigenetic variability, defined for example, in the compartmentalization of their chromosomes is also observed, highlighting that variation beyond genome content likely plays a role in the observed intraspecific functional variability (Yildirim *et al.* 2022).

In addition to uncovering high intraspecific genome variations, high-throughput analysis of DNA isolated from single nuclei has revealed that within the model AMF species, there exist two genetic categories. Specifically, *R. irregularis* strains exist as dikaryons (also referred as heterokaryons) (Fig. 1) or homokaryons (Fig. 2). On one hand, dikaryotic strains consist of thousands of nuclei that are derived from genetically distinct parental strains and exhibit





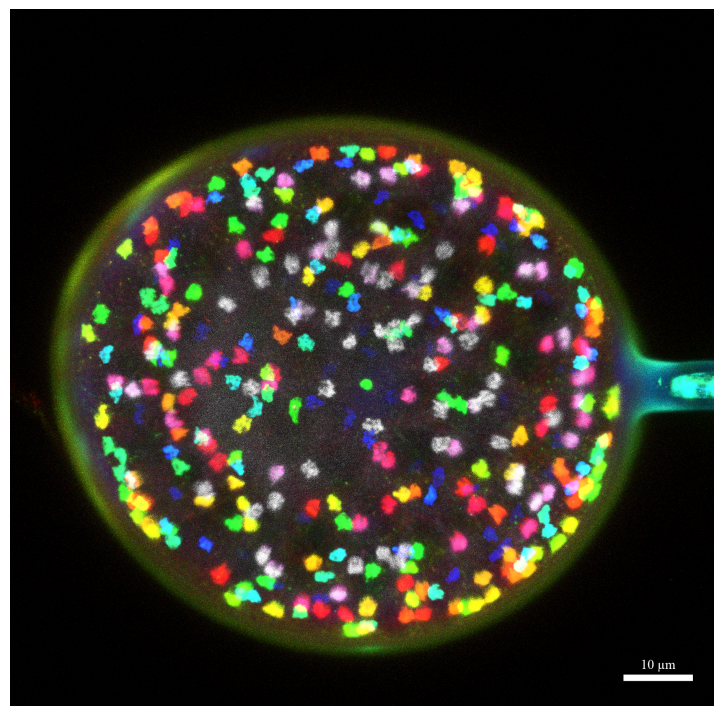
**Figure 1.** Dikaryon AMF spore. Photo by: Vasilis Kokkoris.

divergent genotypes, known as nucleotypes (Ropars *et al.* 2016; Chen *et al.* 2018a; Sperschneider *et al.* 2023). On the other hand, homokaryotic strains possess nuclei with identical genomes throughout. The presence of these two life-cycles in a single AMF cell is reminiscent of the stages seen in the other multinucleate fungi of the Dikarya (Ascomycetes and Basidiomycetes).

Within this context, we hypothesized that the coexistence of two nucleotypes within each cell likely holds functional significance, as the presence of two nuclear types in Dikarya provides significant benefits, including higher fitness (Beadle and Coonradt 1944; Clark and Anderson 2004). Supporting this hypothesis, we found that AMF dikaryotic strains can display unique life history strategies compared to homokaryotic relatives. These include faster extraradical hyphal growth and the capability to establish more intricate extraradical hyphal networks. In contrast, homokaryotic strains seem to exhibit higher spore germination (Serghi *et al.* 2021). But what drives AMF dikaryons to do better? One possibility is

that their genomes provide distinct protein sets and vary in relative abundance across conditions, possibly allowing for greater “functional flexibility” in response to environmental change, compared to homokaryons.

The latter question was recently addressed using digital droplet PCR on thousands of spores isolated from all public (four) AMF dikaryons (Kokkoris *et al.* 2021) - all belonging to *R. irregularis*. These analyses have shown that AMF dikaryons vary in the relative abundance of their two co-existing genomes. In some cases, the genomes differ by up to 80% in relative abundance, meaning that one is obviously dominating the common cytoplasm. In addition to differing in nuclear dynamics, the genetics AMF dikaryons are influenced by host change. For example, while one genome dominates in the cytoplasm in the presence of a certain plant, the same genome can have significantly lower abundance in the presence of another plant (Kokkoris *et al.* 2021). These findings are significant as they highlight an intricate



**Figure 2.** Homokaryon AMF spore. Photo by: Vasilis Kokkoris.

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communication between mycorrhizal partners, which ultimately changes the genetics of the symbiont.

But why do the genomes change in abundance, and what are the consequences for the partners? To address this question, recent analyses have combined high-fidelity long read sequencing with chromatin sequence capture. These demonstrated that two genomes indeed separate among thousands of co-existing nuclei in all AMF heterokaryons and vary in relative abundance (Sperschneider *et al.* 2023). Remarkably, in these strains the two coexisting genomes exhibit significant differences in gene content, with up to 11% of their genome carrying genes specific to one nucleotype. Furthermore, each genome also differs in epigenetic regulations which leads to unique expression profiles under abiotic environmental variation and when entering symbiosis with different plant hosts (Sperschneider *et al.* 2023). Notably, the expression levels of each parental haplotype align with their relative abundance in the mycelium (Sperschneider *et al.* 2023) – i.e. the more abundant genome expresses most of the transcriptome - which is influenced by factors such as the identity of the host plant (Kokkoris *et al.* 2021) and abiotic conditions (Cornell *et al.* 2022).

This unique genetic makeup of the dikaryotic strains led to the intriguing hypothesis that they might be better mutualists compared to homokaryotic strains, which represent the majority of the known strains and, to our current knowledge, the ones used in most biofertilizers. Although still unpublished, we recently tested the mutualistic quality of all the publicly available dikaryotic *R. irregularis* strains and multiple homokaryotic ones when interacting with numerous potato cultivars. In contrast to our

expectations, we found that dikaryotic strains were inferior mutualists regardless of possessing two genomes and being able to regulate their relative abundance even *in vivo* (Terry *et al.* 2023).

We are finally beginning to understand a big part of the extreme plant response variation to inoculation with AMF, as observed across experiments. The fine-scale picture of the genome content and variation within *R. irregularis* now allows the community to build testable genetic hypotheses. In particular, it allows us to determine whether some (epi)genome content or nuclear abundance is better tailored to the growth of a specific crop or leads to significantly higher ecosystem productivity under stress. To do this, it will be important that future studies focus on comparing closely related AMF strains, and perform studies on a much larger variety of hosts and conditions, including under organic farming practices, forestry, and nurseries. Performing detailed transcriptomic analysis will also be essential in order to identify genes that are expressed across hosts and across abiotic conditions, and to detect which regulations and/or presences are linked to desired plant benefits.

Finally, in line with the genetic makeup of other fungal groups (e.g., Basidiomycetes and Ascomycetes), the discovery of homokaryotic and dikaryotic AMF strains alongside the presence of a meiosis toolkit and mating type genes (MAT-loci) (Ropars *et al.* 2016; Kokkoris *et al.* 2021), and the occurrence of rare recombination events (Chen *et al.* 2018a), raise the possibility of a cryptic sexual or para-sexual cycle existing in AMF. The recent advances in AMF genetics (Ropars *et al.* 2016; Chen *et al.* 2018b, c; Kokkoris *et al.* 2021; Serghi *et al.* 2021; Cornell *et al.* 2022; Yildirim *et al.* 2022; Sperschneider *et al.*



2023) together with the updated phylogeny for the model species (Sperschneider *et al.* 2023), now allow us to identify potentially sexually compatible strains, and eventually produce recombined crosses that may be able to outperform current strains for traits that are desirable for agriculture.

In summary, our understanding of how genetic variation influences mycorrhizal response is now emerging. However, there is still much progress to be made in identifying the precise genetic mechanisms that could give rise to strains capable of consistent and successful establishment under various field conditions and across different crops. The level of complexity in research approaches is likely to increase considering that a single plant can host multiple AMF simultaneously. It is crucial for bio-fertilizer industries to actively support this research in AMF genetics, as opposed to promoting single-strain products as universally efficient or miraculous solutions. Failure to deliver on such promises not only harms their own credibility but also undermines the efforts of mycorrhizal researchers dedicated to advancing agricultural and horticultural applications.

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## INVAM is now at the University of Kansas!

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The International Culture Collection of (Vesicular) Arbuscular Mycorrhizal Fungi (INVAM) is the world's largest and most renowned collection of arbuscular mycorrhizal fungal isolates. For four decades, mycorrhizologists worldwide have recognized and utilized INVAM as a valuable resource. The primary objective of INVAM is to serve as a permanent repository of living cultures of arbuscular mycorrhizal fungi (AMF), readily accessible to individuals in need of fungal material for teaching, research, industry development, or technical innovation, all at a reasonable cost. INVAM has been exceptionally successful in achieving this objective, with its fungal strains inspiring numerous contributions to various fields, including AMF taxonomy, comparative biology, systematics, genetics, environmental sequencing interpretation, ecology and biogeography, as well as the practical applications of AM fungi. With an average of 350 germplasm releases each year, INVAM continues to make a significant impact in the scientific community, and its publicly available methodologies have been instrumental in training leading ecologists and their students worldwide. Boasting more than 4,000 citations (Stürmer *et al.* 2021), INVAM maintains a substantial presence both within and beyond the scientific realm.

### INVAM history

The collection was initially established in 1985 by Dr. Norman Schenck at the University of Florida, and under his dedicated leadership, INVAM flourished until 1990. Following Dr. Schenck's

retirement, the INVAM isolates were transferred to West Virginia University, where Dr. Joe Morton and assistant curator Bill Wheeler assumed the responsibility of managing the collection.



*Joe Morton (front) and Sidney Stürmer (back) check out the INVAM collection in its new home at KU during a recent meeting of the INVAM Science Advisory Committee.*

Over the course of 27 years, Joe and Bill expanded the collection to its current size, which includes 996 strains of 103 Glomeromycota species (at least), representing an impressive 30% of known taxonomic diversity. Following Joe's retirement in 2019, Bill Wheeler continued to competently manage the collection, with Dr. Matt Kassin serving as INVAM's Interim Director at West Virginia University. However, with Bill's impending retirement, it became crucial for the collection to have the guidance of an AMF



mycologist. After securing a National Science Foundation infrastructure grant to support the transfer of the living collection, INVAM commenced its relocation to the University of Kansas at the end of 2021.

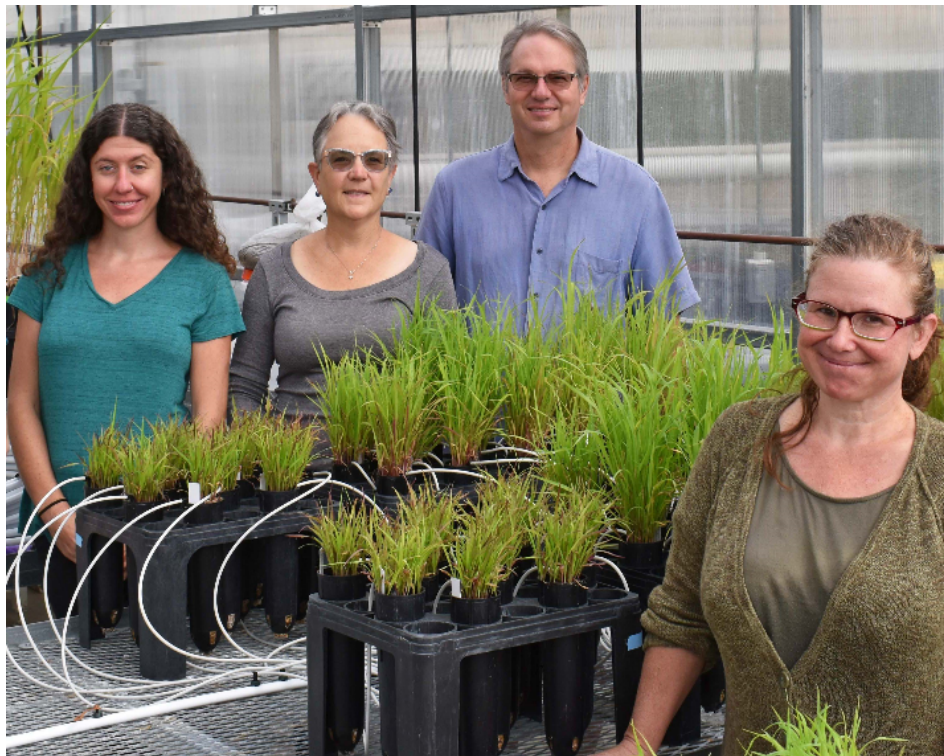
### Meet the new INVAM team at KU

INVAM is now located at the University of Kansas (KU), specifically at the Kansas Biological Survey and Center for Ecological Research. You can visit their website at (<https://invam.ku.edu/>). The team at INVAM is led by curators Dr. James Bever and Dr. Peggy Schultz, along with assistant curators Dr. Liz Koziol and Dr. Terra K. Lubin. Dr. James Bever serves as the lead curator of INVAM and holds the position of Foundational Distinguished Professor at KU. In 2021, he received the prestigious IMS Eminent Mycorrhiza Research Award at ICOM 11 (International Conference on Mycorrhiza) for his significant contributions to mycorrhizal research and plant-soil feedbacks, among other fields. When asked about the INVAM move to KU, Dr. Bever

expressed his enthusiasm, stating “preserving the biological resources built by Dr. Morton is critical to the advancement of research and understanding of AMF biology, ecology and systematics”.

Peggy Schultz is a co-curator of INVAM and serves as an Associate Specialist in the Center for Ecological Research and Environmental Studies Program at KU. Much of Peggy's research focuses on environmental education and community outreach. Her expertise in these areas is invaluable as INVAM continues to build on its tradition of outreach and education.

Liz Koziol, an Assistant Research Professor at KU, is an associate curator of the INVAM collection. Liz has worked closely with Dr. Bever and Peggy Schultz for 13 years as a lead curator of the lab's AMF collection, which consists of nearly 60 isolates of AMF isolated from US prairies. Liz utilizes these prairie endemic AMF isolates to conduct applied research on prairie



*The core INVAM team, from left to right: Drs. Liz Koziol, Peggy Schultz, Jim Bever, and Terra Lubin. In the foreground are some of the INVAM mycorrhizal cultures. Photo by: Kirsten Bosnak.*

restoration diversity, improving perennial and organically grown crop productivity, and investigating plant phytochemistry. When it comes to INVAM, Liz says, "Of course, the jump from maintaining 60 isolates to 1060 isolates a year is a major change! However, our team rocks, and after the first year, we are already running smoothly".

Terra Lubin, a Post-doctoral researcher at KU, serves as an Associate Curator of the INVAM collection. Terra is the behind-the-scenes maestro of INVAM logistics, overseeing the daily maintenance of the collection since its transfer to KU. Terra also took the lead in creating the new INVAM website and online store. She is incredibly excited about the utility of the new online store and expects it to be up and running by the second semester of 2023.

### **INVAM's first full year at KU**

Since its move to the University of Kansas (KU) in 2021, INVAM has successfully completed two full rounds of the nearly 1,000 AMF accessions in the KU greenhouses. We are delighted to announce that KU INVAM accessions are now available to the public, and we are offering standard services such as MIP and spore extraction. To place an order, please visit (<https://invam.ku.edu/ordering>) for detailed ordering instructions. For inquiries regarding INVAM services, we recommend exploring our website and FAQ section before reaching out to [invam@ku.edu](mailto:invam@ku.edu). Our dedicated Team members will be glad to assist you promptly.

One of the key directives from NSF in moving INVAM to KU was to modernize the fee structure, ensuring the financial stability of the collection while maintaining reasonable costs for users. You can find the updated fee structure on our website, providing transparency and clarity for

Expe accessing the INVAM collection.

Beyond the essential tasks of culture propagation and release, the shift to KU brought a paramount goal of maintaining and enhancing the INVAM website, now housed at <https://invam.ku.edu/>. INVAM's webpage serves as a comprehensive repository of standardized methods for growing AMF, including protocols for working with spores, roots, infectivity assays, and DNA analysis. Additionally, we have rescued the detailed descriptions of the spore morphology of 81 AMF species written by Joe Morton, representing approximately 25% of the currently described species within the phylum. These descriptions are accompanied by high-quality photographic representations of important taxonomic characters, making our website a valuable and extensive resource that has been continuously developed over the past 38 years. Looking ahead, the INVAM Team is eager to expand the website by adding more species descriptions and educational tutorials. Stay tuned for these exciting updates in the coming months!

We warmly welcome any questions and feedback as we continue to develop new programs and seek new funding sources to support this vital work. Your engagement and support are invaluable to us as we strive to advance the field of mycorrhizal research and promote the understanding of fungal symbiosis in plant ecosystems.

### **References**

- Stürmer SL, Bever JD, Schultz PA, Bentivenga SP. 2021. Celebrating INVAM: 35 years of the largest living culture collection of arbuscular mycorrhizal fungi. *Mycorrhiza* 31:117-126.  
<https://doi.org/10.1007/s00572-020-01008-z>

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## YouTube interviews\*

### - **Katie Field on nutrient exchanges between `fine root endophytes` & a flowering plant**

Prof. Pedro M. Antunes (Algoma University, Canada) interviews Prof. Katie Field (University of Sheffield, UK) about the first evidence that fine root endophytes (phylum Mucoromycotina) are nutritional mutualists with a flowering plant. In other words, these fungi are mycorrhizal.

Interview: <https://southmycorrhizas.org/reading/april-2023/>

Study: Hoysted GA, Field KJ, Sinanaj B, *et al.* 2023. Direct nitrogen, phosphorus and carbon exchanges between Mucoromycotina ‘fine root endophyte’ fungi and a flowering plant in novel monoxenic cultures. *New Phytol* 238:70-79.

<https://doi.org/10.1111/nph.18630>

### - **Laura van Galen on correlated evolution between *Nothofagus* & its ectomycorrhizal symbionts**

Prof. Natalia V. Fernández (Universidad Nacional del Comahue, Argentina) and Prof. César Marín (Universidad Santo Tomás, Chile), interview Laura van Galen (Postdoc at ETH Zurich in the Crowther Lab), about correlated evolution in an ectomycorrhizal-host system.

Interview: <https://southmycorrhizas.org/reading/april-ii-2023/>

Study: van Galen LG, Orlovich DA, Lord JM, *et al.* 2023. Correlated evolution in an ectomycorrhizal host–symbiont system. *New Phytol* 238:1215-1229.

<https://doi.org/10.1111/nph.18802>

**\*Section by:**

**South American Mycorrhizal Research Network**

Contact/Join us: <https://southmycorrhizas.org/join/>



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# Tools

## → **MitoGeneExtractor: extracting mitochondrial genes from NGS libraries**

Brasseur *et al.* (2023) developed a tool that allows to extract mitochondrial protein coding genes of interest from next generation sequencing libraries through multiple sequence alignments of sequencing reads to amino acid references

Study: Brasseur MV, Astrin JJ, Geiger MF, Mayer C. 2023. MitoGeneExtractor: Efficient extraction of mitochondrial genes from next-generation sequencing libraries. *Methods Ecol Evol* 14:1017-1024.

<https://doi.org/10.1111/2041-210X.14075>

## → **igraph: R package for network analysis**

Csárdi *et al.* (2023) provide an R version of the python-based tool, igraph, which can handle large graphs very well and provides functions for generating random and regular graphs, graph visualization, centrality methods and much more.

Study: Csárdi G, Nepusz T, Traag V, *et al.* 2023. *igraph: Network Analysis and Visualization in R*. R package version 1.5.0.1,

<https://CRAN.R-project.org/package=igraph>

## → **promor: R package for proteomic data**

Ranathunge *et al.* (2023) present *promor*, a comprehensive, user-friendly R package that streamlines label-free quantification proteomics data analysis and building machine learning-based predictive models with top protein candidates.

Study: Ranathunge C, Patel SS, Pinky L, *et al.* 2023. *promor: a comprehensive R package for label-free proteomics data analysis and predictive modeling*. *Bioinform Adv* 3:vbad025. <https://doi.org/10.1093/bioadv/vbad041>

**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), [Vol3\\_I2](#) (p. 17), [Vol3\\_I3](#) (p. 26), and [Vol4\\_I1](#) (p. 19).

## Events

### MYCORRHIZAL EVENTS:

#### III International Symposium on Mycorrhizal Symbiosis in South America

##### Website

Instituto SINCHI, Leticia, Colombia – Hybrid  
28 – 30 August, 2023

Organizers: South American Mycorrhizal Research Network and Instituto SINCHI



#### Symposium on Population and Landscape Genomics of Ectomycorrhizal Fungi

##### Website

WSL, Zurich, Switzerland – Hybrid  
5 – 6 September, 2023

Organizers: Ben Dauphin, Martina Peter



- The 6<sup>th</sup> international Molecular Mycorrhiza Meeting will take place in Cambridge, United Kingdom, 25 – 27 September, 2023.

Further information in Twitter: [@slcuplants](#)

- The 12<sup>th</sup> International Conference on Mycorrhiza (ICOM12) will take place in Manchester, United Kingdom, 6 – 11 August, 2024.

Further information in Twitter: [@ICOM\\_12](#)

- The 13<sup>th</sup> International Conference on Mycorrhiza (ICOM13), will take place in Cairns, Australia, in 2026. Stay tuned for further information.

### MYCOLOGICAL EVENTS:

#### 12<sup>th</sup> International Mycological Congress

##### Website

MECC, Maastricht, the Netherlands  
11 – 15 August, 2024



Organizers: Local & International organizers and International Mycological Association.



## OTHER EVENTS:

### Organic Phosphorus Workshop 2023

#### Website

Universidad de La Frontera, Pucón, Chile  
27 November – 1 December, 2023

Organizers: BIOREN – UFRO.



### 2023 British Ecological Society Annual Meeting

#### Website

ICC, Belfast, United Kingdom  
12 – 15 December, 2023

Organizers: British Ecological Society.



## AWARD CALL:

### ABOUT

The award is honoring frontier and cutting-edge science related to how we can harness the power of fungi to solve some of humanity's largest environmental challenges.

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- Mentorship from experts in the field
- Access to valuable network
- Increased visibility and recognition

APPLICATIONS OPEN FROM 5<sup>TH</sup> of Sept  
Winners are announced the 23<sup>RD</sup> of November

FOR MORE INFO VISIT: [WWW.FUTUREISFUNGI.ORG](http://WWW.FUTUREISFUNGI.ORG)



<https://www.futureisfungi.org/>

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## IMS Newsletter

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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.