***In-situ* mycorrhizal function - knowledge gaps and future directions**

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**Summary**

We know a lot about the *potential* functions of mycorrhizas, but whether or not these are *realized* in the field where plants simultaneously experience a range of biotic interactions and fluctuating abiotic conditions is more or less unknown. In this viewpoint, we present findings from a literature survey of papers on mycorrhizal function published in New Phytologist during the past thirty years. This survey showed that most functional studies are still conducted under controlled conditions, target mostly arbuscular and ectomycorrhizas, and focus on nutrient and carbon dynamics of the symbiosis. We also share discussions from a workshop, “*In-situ* mycorrhizal function: how do we get relevant data from a messy world?”, held at the 9th International Conference on Mycorrhiza (ICOM) in August, 2017. In this workshop, we examined possibilities and limitations of old and new techniques for field research, and participants expressed the need to learn more about fungal traits and how they may relate to function. We argue that moving mycorrhizal experiments into the field will allow us not only to quantify realized functions, but also to revisit old paradigms and possibly discover new functions.

**Keywords (5-8):** Mycorrhizal function, field, methods,arbuscular mycorrhizas, ectomycorrhizas

**Background**

Since research on mycorrhizas began, we have learned a great deal about the taxonomic identity and richness of the symbiotic partners, as well as their form and potential function (Smith & Read, 2008). Most functional studies have targeted nutritional benefits to the host of the symbioses, and groundbreaking work has shown that fungal symbionts can provide the majority of nutrients required by plants (Smith *et al.*, 2003) and access to nutrient sources that are otherwise unavailable to them (Read & Perez-Moreno, 2003). Persistent debates remain about functional diversity and complementarity, evolution and selection of function, and host-fungus interactions operating along the mutualism to parasitism continuum to name a few. The most striking gap in our opinion, however, is the weak knowledge of the functional properties of mycorrhizas in field settings. In this viewpoint, we highlight the current state of research on mycorrhizal function, identify obstacles to field research, and outline critical questions and approaches we believe can move the field beyond *potential* to *realized* mycorrhizal function. These ideas are partly based on outcomes of the workshop, “*In-situ* mycorrhizal function: how do we get relevant data from a messy world?” that we held at the 9th International Conference on Mycorrhiza (ICOM) in August, 2017. Moving mycorrhizal research into the field involves many challenges, but will allow us not only to quantify realized functions, but to revisit and examine old paradigms, and potentially discover new functions.

**Current state of research on mycorrhizal function**

To get a better idea of the nature of functional mycorrhizal research, we searched Web of Science on October 15th, 2017, using the option “All Databases” and the search terms “Mycorrhiza\* and function” restricted to New Phytologist papers published between 1987-2017. We chose to focus on New Phytologist publications due to the journal’s long history of publishing high-quality, mechanistic mycorrhizal research. This returned 212 publications, but 145 of those were rejected because they were reviews, commentaries, or clearly addressed a separate topic. For the remaining 67 papers, we collected information regarding mycorrhizal type studied, the function targeted, whether individual fungi or communities were included, how the symbiosis was manipulated, what measurements were collected, and whether the study was conducted in the greenhouse, field or involved axenic cultures (see Supporting Information Table S1 for specific papers included and information extracted and Table S2 for a summary). This was by no means meant to be exhaustive, and there clearly are well-known functional papers that were excluded because they were published elsewhere or were not targeted by our search terms. However, we argue that these publications include a relevant subset of high-quality mycorrhizal studies published during the past 30 years that illustrate specific functions and symbioses researched, as well as approaches chosen.

Not surprisingly, most studies targeted ectomycorrhizas (EM, 48%) and arbuscular mycorrhizas (AM, 48%) while ericoid and orchid mycorrhizas were the focus in <5% of studies. Likewise, nutrient (67%) and carbon (40%) movements were the main functions assessed, whereas other functions, such as water relations (7%) and pathogen protection (1%) were rarely studied. This is particularly interesting given the recent Delavaux *et al.* (2017) meta-analysis showing that services other than nutrient acquisition can be equally important in AM, and results by Bennett *et al.* (2017) highlighting the central role of pathogen protection by EM fungi. Mycorrhizas were most often manipulated using inoculation (46%), whereas ingrowth cores (10%) and fungicides (4%) were less utilized. The use of genetic manipulation (e.g., knock out or expression systems) to reveal function was restricted to EM in these publications (14%), although plant mutants have been very informative in AM research published elsewhere (e.g., Barker *et al.*, 1998; Javot *et al.*, 2007). Some experiments (31%) relied on other manipulations, such as CO2 enrichments or nutrient amendments, which indirectly manipulated mycorrhizal fungal abundance or composition, and thus limited assessments of mycorrhizal function to correlation analyses between mycorrhizal responses and other variables measured.

Most studies measured biomass responses by both plants and fungi (Fig. 1; Supporting Information Table S1). While biomass represents the consequence of the sum of all functions, it provides limited information about the underlying mechanism(s) unless paired with specific treatments, such as nutrient additions or water manipulations. Also, biomass may not be a good measure of fitness (Varga & Kytöviita, 2010), especially when extrapolated from short-term greenhouse experiments. To understand mechanistic relationships, it is essential to distinguish between the measurement of actual function and various proxies of function. This applies to other variables as well. For instance, genomic studies need to be combined with host or fungal mutants or other experimental approaches to verify actual, not just potential, function. Likewise, solely quantifying differences in enzymatic activity between mycorrhizal and non-mycorrhizal treatments may have limited value unless it is combined with some measure of how shifts in activity influence either plant or fungus.

The most striking finding from the literature survey, however, was that—despite pleas by other researchers more than twenty years ago (Read, 1991; Johnson *et al.*, 1997)—we are still primarily conducting experiments in controlled environments, not in the field. Of the 67 studies we surveyed, only three experimentally manipulated mycorrhizal abundance in the field. These studies used rotating soil cores (Johnson *et al.*, 2001) or transplanted seedlings of varying AM colonization (McGonigle & Fitter, 1988) to quantify the role of AMF for P acquisition, or applied fungicides to assess the role of ericoid mycorrhizal fungi in heath (Michelsen *et al.*, 1999). None of these are recent publications, which highlights the fact that while methods to manipulate mycorrhizal fungal abundances in the field are available, their use continues to be limited.

**What are the barriers to field research?**

The keywords “Experiment” and “greenhouse/chamber” were positively correlated and opposite to “field” and “survey” when relationships among the 67 New Phytologist publications were assessed (Fig. 1, Supporting Information Table S1). In other words, we tend to conduct experiments under controlled conditions, and surveys in the field. Surveys can be powerful tools to understand relationships between mycorrhizas and various processes (e.g., Read, 1991; Cheeke *et al.*, 2017), but in order to quantify function, we need to experimentally manipulate the symbiosis. This is often quite challenging to do in the field. Inoculating larger areas can be costly and impractical and relies on low natural abundances of fungi, fungicides reduce the abundance of all fungi, which complicate interpretations, and rotating soil cores take a lot of maintenance to be effective. In addition to technological challenges associated with field experiments, conditions are harder to control in the field than in the greenhouse, and plants and fungi are sometimes exposed to multiple biotic interactions and varying abiotic conditions that can reduce the likelihood of significant responses. The logistical issues inherent in field research are compounded by the fact that access to existing long-term field experiments and the creation of new ones are sometimes challenging. This dissuades many researchers, especially early career scientists, from embarking on field experiments. Joining global research collaborations, such as Nutrient Network ([www.nutnet.umt.edu](http://www.nutnet.umt.edu)), or conducting add-on studies in established Long Term Experimental Research (LTER) sites (<https://lternet.edu>) may be ways to circumvent obstacles and reduce cost, save time and minimize risks associated with field experiments.

Our visualization of the papers illustrated another potential barrier to progress and paradigm shifts in mycorrhizal research. In Figure 1, AM and EM were clearly separated from each other, and so were many of the methods used, indicating that different symbioses are often researched in isolation using a specific set of tools. While this may be appropriate in cases where one symbiosis dominates, recent papers highlight how much we can learn from comparing symbioses using the same methodology (Bennett *et al.*, 2017 and Cheeke *et al.*, 2017). This is not only an issue across symbioses, but also applies to different disciplines within a symbiosis. For example, many fungal community surveys implicitly assume that observed shifts have functional consequences, whereas studies assessing function often research responses using selected fungal isolates or undefined mixed inocula that lack obvious links to field systems (Supporting Information Table S1). Based on this, it was encouraging to see the increased crosstalk across disciplines at ICOM 9 (Waller *et al.*, 2018), which we hope will reduce real or perceived divisions, enable transfer of methodology and expertise, and result in novel and creative ways of answering research questions.

**What can we learn from field research and what are feasible approaches?**

The field of evolution probably offers the best example of the importance of studying organisms in their natural environments. For example, how would we make sense of the shift in melanism in peppered moths were it not for the observation of concomitant changes in soot pollution combined with controlled predation experiments (summarized in Cook *et al.*, 2012)?

What are the unanswered questions in terms of mycorrhizal function, and how would our perception of the symbiosis change if we were better able to capture function in the field? Are mycorrhizal fungi parasitic in nature and if so, to what extent, under what conditions and for what duration? Participants at the ICOM 9 workshop were asked to identify unanswered questions related to mycorrhizal function, and we captured responses as word clouds (Fig. 2a). The key knowledge gaps centered around mycelial traits, highlighting how the fungal mycelium remains a critically important but poorly understood component of the symbioses that we rarely measure (Fig 2a). Mycelial growth and colonization patterns differ among fungal taxa, both within AM and EM (Agerer, 2001; Hart & Reader, 2002; Koide *et al.*, 2007 and references therein), and these differences may translate into different functions (Courty *et al.*, 2005; Maherali & Klironomos, 2007). For example, AM fungi that predominately colonize inside the root may be better pathogen protectors than those that grow an extensive extraradical mycelium, which aids in nutrient uptake (Maherali & Klironomos, 2007). The former group appears to replace the latter as soil fertility increases, and this coincides with less beneficial plant responses in greenhouse experiments (Johnson, 1993). While parasitic relationships are certainly possible (Johnson *et al*., 1997), it is also conceivable that AM fungi from fertilized soils provide a different function, such as pathogen protection, which is seldom assessed in greenhouse experiments. We could test this along natural or imposed fertility gradients by combining genomic approaches that target genes associated with nutrient uptake and defense with treatments specifically designed to quantify nutrient acquisition and pathogen protection by AM fungi. These studies could be combined with fungal community analyses and manipulations of fungal abundance and possibly reciprocal transplant experiments (Johnson *et al.*, 2010). While daunting, there is an urgent need to determine to what extent functions differ among taxa across all symbioses, and which plant and fungal traits, if any, predict these differences (Sikes *et al.*, 2009). We also need to quantify the relative importance of fungal abundance vs. community composition, and whether different functions and communities can be predicted based on biotic and abiotic conditions. If we can make these predictions, then community analyses could finally become a proxy for function, but we have a long way to go before that is the case.

Linking functional traits and composition is challenging for many reasons (van der Heijden & Scheublin, 2007), but studies that have combined these approaches have been informative. For example, Helgason *et al.* (2002) showed that the most abundant isolate of arbuscular mycorrhizal fungus colonizing *Acer pseudoplatanus* in the field was also the most beneficial when inoculated onto *A. pseudoplatanus* under controlled conditions. This suggests that the non-random distribution of AM fungi in that system is driven by selective carbon allocation to the better mutualist (*sensu* Kiers *et al.*, 2011) rather than competitive interactions among fungi where the more competitive fungus (that may also be the poorer mutualist, Bever *et al.*, 2009) wins. The Helgason *et al*. study also highlights the benefit of combining surveys and controlled experiments. Other examples of papers that have linked function and composition include Walker *et al.* (2014), which measured enzyme activities of individual EM root tips coupled with molecular analyses to identify the fungus involved, and Clemmensen *et al.* (2015), which combined high throughput sequencing and observations of EM fungal growth forms and decomposability to help explain shifts in C and N sequestrations along a boreal chronosequence. These studies are noteworthy because they not only quantified the extent of functional differences among fungal species, but also linked those differences to specific traits and distribution patterns. These studies indicate that much can be learned about mycorrhizas in field settings without having to manipulate fungal abundances when this proves to be too challenging. Another approach that requires no manipulations of fungal abundance is reciprocal transplant experiments where local adaptation in the mycorrhizal symbioses can be assessed (Johnson *et al.*, 2010). Overall, in order to better understand mycorrhizal function, we need to use a consortia of methods and approaches, including surveys, reciprocal transplants, and experiments that manipulate fungal abundances.

**The utility of existing and emerging technologies**

During the ICOM 9 workshop, we discussed current and emerging technologies available to quantify mycorrhizal function in more natural settings. Organizers and invited speakers highlighted ways to manipulate mycorrhizal fungal abundances in the field using fungicides and ingrowth cores (Ylva Lekberg), as well as the potential use of mutants (Thomas Irving), radioactive isotopes (Katie Field), enzymes (Björn Lindahl), and quantum dots (Victor Caldas ), to study mycorrhizal function, nutrient transformation, uptake and movement. Thorunn Helgason outlined the potential use of genomic approaches, and Edith Hammer described a new technology that mimics the complexity of soils to increase realism in laboratory studies (Aleklett *et al.*, 2017). Finally, Gaby Deckmyn reminded us all that in order to make full use of modelling, we need to collect more and better metadata (particularly environmental) during our surveys and experiments (Deckmyn *et al.*, 2014).

Following these presentations, participants were asked what methods to use to address unanswered questions regarding mycorrhizal function highlighted above. Two themes emerged: 1) the application, in the field, of techniques typically confined to the laboratory, such as biomolecule analyses including various -omics approaches (genomics, transcriptomics and proteomics), and 2) the development of ways to capture the behaviour of the mycorrhizal symbiosis directly. Most commonly highlighted were ways to image the symbiosis in the field and to develop and increase the range of biomarkers used to trace function (Fig 2b). This could be done using cutting-edge technology, such as the “lab on a chip” microfluidics and quantum dots (Aleklett *et al.*, 2017), as well as established methods, such as minirhizotrons (Hendrick & Pregitzer, 1996) and signature fatty acids (Olsson & Johnson, 2005). The latter two can be combined with C-isotopes to inform on C allocation specifically to mycorrhizal fungi (Bending & Read, 1995; Olsson & Johnson, 2005).

Workshop participants also highlighted the potential use of CRISPR gene editing technology (Ran *et al*., 2013). Mutants have provided invaluable insight into mycorrhizal functioning, and are beneficial because they circumvent the necessity to remove mycorrhizal fungi via fungicide applications or fumigations. The utility of mutants was clearly shown recently using the *rmc* tomato (*Solanum lycopersicum* L., Barker *et al.*, 1998) in a California drought experiment conducted in the field (Bowles *et al.*, 2016). However, the release of GMOs that incorporate genetic information from other organisms into the field poses potential risks and is strictly regulated (if permitted at all). The use of CRISPR has been raised as an alternative to GMOs in field research given that no foreign material is added, but there is currently little consensus among countries regarding gene-editing rules (Nature editorial, 2017). As such, researchers should check specific regulations in their country.

While it is tempting to wait for/rely on new technologies, many of which were highlighted by workshop participants, existing ones can help us answer important questions. For example, in 1982, Chiarello *et al*. published a groundbreaking paper in Science that tracked 32P movements within a grassland, possibly via arbuscular mycelial networks; and in 1997, Simard *et al*. used 13C and14C to assess C movements among trees in the field. Both studies stimulated subsequent research on common mycorrhizal networks. More recently, however, the use of radioactive isotopes has been largely confined to very controlled conditions (e.g., Mikkelsen *et al.*, 2008). This is understandable given restrictions in many places against radioactive isotopes (33P may have fewer restrictions given the lower radioactivity), but it is unfortunate given that 32P and 33P applied in hyphal ingrowth bags (Johnson *et al.*, 2001) could measure mycorrhizal P uptake in natural systems (Jakobsen, 1994) so long as appropriate precautions are taken to minimize risk. Combined with carbon isotopes (13C or 14C), we could repeat elegant cost-benefit assessments conducted in the greenhouse more than two decades ago (Pearson & Jakobsen, 1993). Overall, the issue is not necessarily that we need new methods, but that we applyavailable methods *in the field* wherever possible*.*

**Summary**

Ernst Mayr said, “The history of science knows scores of instances where an investigator was in possession of all the important facts for a new theory, but simply failed to ask the right question” (Mayr, 1982). Our workshop and literature survey revealed that there are a suite of “typical” approaches that we use to study mycorrhizal function, most of them under controlled conditions, and that there are significant barriers to conducting field research. However, these obstacles are not insurmountable, and moving mycorrhizal research into the field will allow us not only to quantify realized functions, but also to revisit and examine old paradigms and potentially discover new functions. Mycorrhizas could have very important roles to play in the future, including mitigating the decreasing reserves of phosphorous fertilizers, and helping plants tolerate the increasing stress associated with more severe droughts predicted with climate change. With creativity and ambition, we can apply old and new tools to field systems, and move into the next decade carrying out transformative experiments that will begin, finally, to answer fundamental questions about what mycorrhizas *actually* do, rather than simply what they are *capable* of doing. Only then can we communicate the possibilities and limitations associated with these symbioses to people outside our field.

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**Author contributions**

Authors contributed equally to the work presented here.

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**Supporting information:**

Table S1. Information extracted from papers in our literature survey

Table S2. Summary of information gathered in our literature survey

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**Figure 1**. PCA biplot implemented in the Vegan package of R, using the data in table S1, excluding uninformative variables occurring 10 times or fewer. Grey points represent each paper, and arrows the strength of the variable. For visual clarity, some variables have been renamed: A = Other manipulations, B = Nutrient dynamics, C = Plant nutrient concentration.

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**Figure 2.** Word cloud describing results from workshop participants answering the question 1) What is the most important mycorrhizal function to research (a) and 2) How can this be done (b)?