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Can mycorrhizal fungi fix farming? Benefits and limitations of applying them to agroecosystems

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The intensification of agriculture over the past decades has helped increase crop yields but has also led to various environmental issues, potentially undermining future productivity. One of the options considered for increasing the sustainability of agriculture is the stimulation or enhancement of microorganisms that associate with plants and help them acquire more nutrients from the soil leading to benefits such as increased growth. One key player considered are arbuscular mycorrhizal fungi (AMF), a group of below-ground fungi that form symbiotic relationships with the vast majority of land plants. However, evidence from lab and field trials suggests that not all plants respond equally to colonization by these fungi, and research is on-going to better understand the context-dependency of the symbiosis. Moreover, introducing AMF to agricultural fields through the application of commercial inoculants that contain fungal spores and hyphae has been inconsistent in their desired effects of boosting crop yield and quality. Recently, a quality framework has been put forward to try and increase the reliability of these inocula so farmers can make better use of them. Although further research on the fundamental and applied aspects of plant–arbuscular mycorrhizal associations is required, agricultural practices that favour these fungi should be encouraged as they are likely to lead to wider benefits and ultimately contribute to a more sustainable agricultural system.

Can mycorrhizal fungi fix farming? Benefits and limitations of applying them to agroecosystems

Since the establishment of agriculture over 10,000 years ago, the global human population has come to rely on farming for food production. Development of new agricultural techniques and innovation has meant that yields have continuously increased in line with the human population. Specifically, the 'Green Revolution' of the late 20th century took advantage of technological advances, including breeding of high-yielding crop varieties and the development of pesticides and artificial fertilizers, driving increases in crop yields to meet global demand.

Now, yields seem to have plateaued and arable land has been significantly impacted by decades of intensive agricultural practices. For example, mineral fertilizers not only require a huge amount of energy for production, but the raw resources are also often finite, and their widespread application leads to environmental issues such as the eutrophication of watercourses. Repeated mechanical tilling and turning of soils, another common practice in modern agriculture, breaks down the soil structure and can impede soil water retention and reduce carbon storage, with further downstream impacts on runoff, soil erosion, and ultimately the capacity of soil to sustain life.

Fungi are important for biodiversity and central players in the functionality of soils. One group of soil fungi that are thought to suffer from modern agricultural practices are the arbuscular mycorrhizal fungi (AMF). AMF form symbiotic relationships with the roots of most plant species, known as mycorrhizas. They largely consist of fine thread-like filaments called hyphae, which enter plant roots and penetrate cell walls. Once inside root cells, AMF hyphae form highly branched, tree-like structures, known as arbuscules, which facilitate nutrient exchange between the fungus and the plant host. AMF hyphae spread outwards from the host plant roots, assimilating soil nutrients that they transfer to their hosts. In return, fungi receive

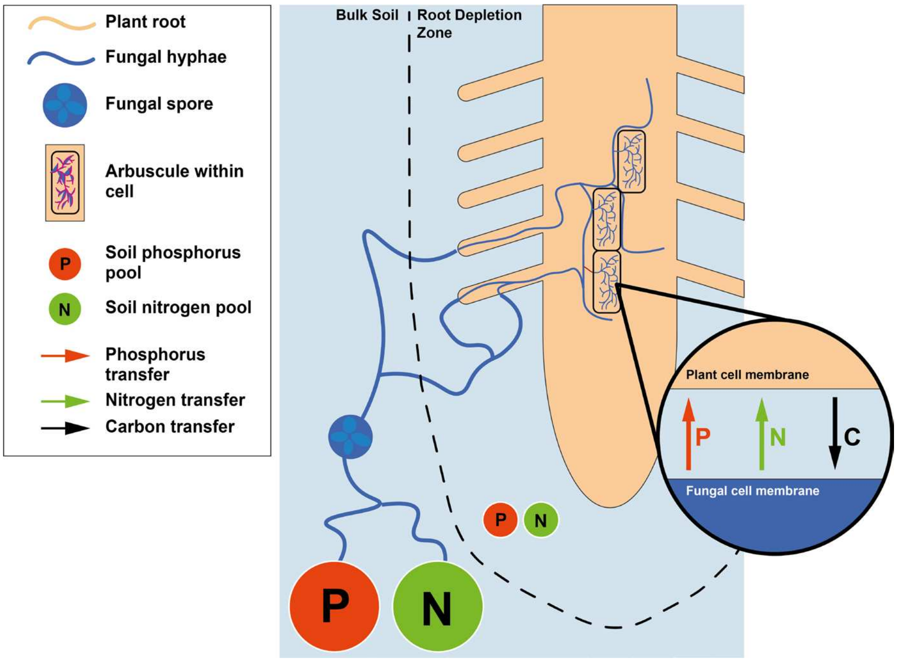

Figure 1. Nutrient exchange between AMF and plant roots.

photosynthetically fixed carbon-based molecules from the plant (Figure 1).

Plant responses to AMF are context-dependent

The nutritional mutualism that underpins plant–AMF symbiosis suggests its application offers a promising approach to improving crop nutrition. Many lab and field studies have demonstrated the potential benefits of AMF on soil function and crop yields. AMF hyphae grow beyond the root nutrient depletion zone and, being much finer than plant roots, can access soil pores containing plant essential nutrients that would be otherwise inaccessible to their host. By harnessing this ability of AMF, there is potential to reduce reliance on synthetic fertilizers. In addition to their nutritional role, AMF can help their plant hosts deal with biotic and abiotic stressors (Figure 2). Research on many crops such as tomatoes and potatoes has shown that plants colonized by AMF can better resist and/or tolerate pests and pathogens. Plant defence signals might even be carried below ground, via mycorrhizal networks, to 'warn' neighbouring plants of pests although the mechanisms remain unresolved and research showing the significance of this at a field scale is lacking. AMF can also make host plants more resilient to drought and help sustain their growth in contaminated (e.g., heavy metal) soils.

Despite the great potential of exploiting crop–AMF symbioses to enhance food production sustainably, the outcomes tend to be very variable and dependent on environmental factors and on the species – and even genotypes – of plants and AMF involved. Crops such as potatoes, for example, seem to show AMF-mediated growth responses more consistently than wheat and other grain crops. The lack of responsiveness of the latter can be partly attributed to selective breeding of varieties for yield-related traits, which often contrast with receptivity and responsiveness to AMF. The capacity for AMF to mediate-growth responses is also often compromised by conventional farming practices such as tillage, which sever the fungal hyphae and potentially restrict the functionality of AMF. Evidence suggests that tillage also affects the mycorrhizal community structure; however, the community might still be able to rapidly recover after disturbance ceases.

Other pressures that may reduce mycorrhizal fungal diversity and functionality are the use of fertilizer and crop rotations with plants that do not typically host AMF, such as brassicas. In general, the application of fertilizers is thought to have a greater effect on AMF community structure than tillage alone although the implications of this in terms of the plant-growth capacity have not been extensively evaluated. Finally, fields with a diversity of crop species of various functional groups (annual/perennial, legume/grass, etc.) may promote the diversity of AMF. However, it is again unclear how exactly this increased AMF diversity might relate to agricultural productivity. AMF can enhance the stability of grassland plant productivity over time so they might have an increased role under predicted future climate perturbations.

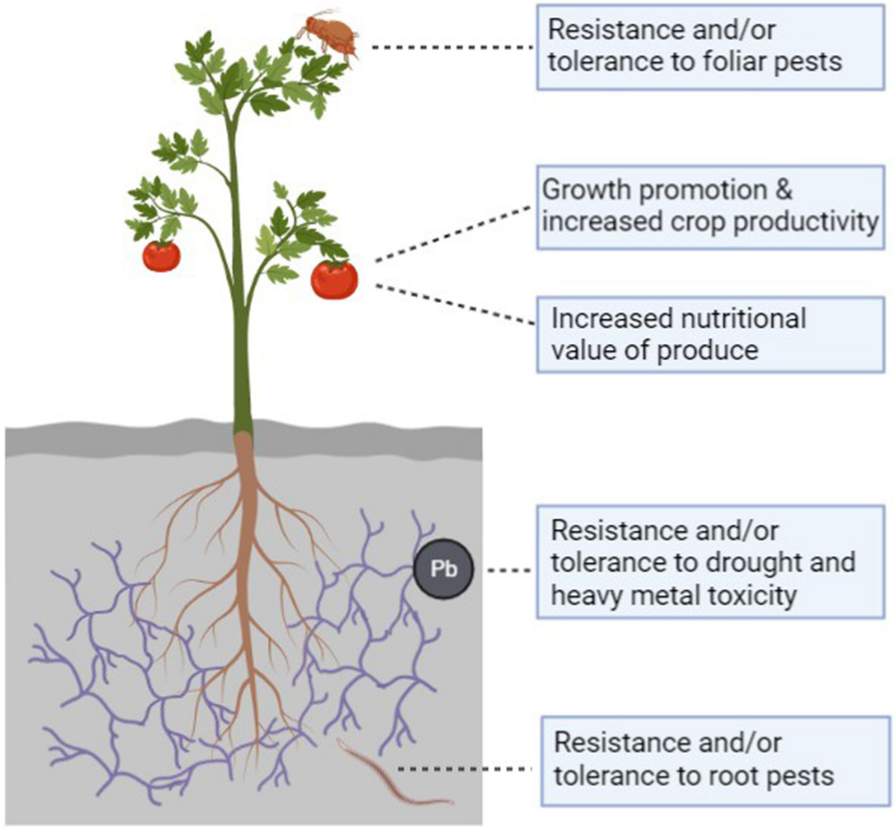

Figure 2. Potential AMF-mediated plant benefits. Content and figure adapted from Jacott et al. (2022), which is available under Creative Commons Attribution 4.0 International License.

Commercial mycorrhizal inoculants require improvement

AMF exist naturally in most soils, but to boost the density of AMF, farmers often use commercially available products that consist of a carrier medium mixed with viable spores and hyphae. Inoculation methods vary but, in general, these products are applied to fields prior to or in conjunction with seeds to – in theory at least – help colonize crop plants at an early stage of their growth and thus maximize any benefits over time. This is a simple and attractive method particularly as prices of artificial fertilizers have increased due to the rising unavailability of raw resources and increasing energy prices. In line with increasing demand, the range of such microbial inoculants has grown, with their global market value forecasted to reach as much as US$11.45 billion by 2026. Some products contain a single AMF species, others use a mixture and around 20% include other beneficial microbes, such as nitrogen-fixing bacteria. With such a variety of products available, it is important that AMF inocula are not considered a 'one size fits all' solution to improving crop yields.

When treated with AMF-containing inoculants, improvements in crop productivity have often been somewhat disappointing compared with the expectations set by greenhouse and lab trials. Within lab trials, environmental factors are tightly regulated whereas, in the agricultural field, dynamic microbial communities and soil nutrient content likely drive the differences in benefits observed between field and lab trials. Researchers attempting to bridge this gap have found that the application of commercial inoculum frequently does not increase mycorrhizal colonization of host plants or plant productivity. A growing body of evidence suggests that the use of microbial inoculants should be considered on a case-by-case basis as their success in colonizating crop plants is dependent on crop species, native microbial communities, soil type and whether the soil has received excessive amounts of fertilizers. Further field trials are needed to better understand the factors impeding consistently positive plant responses to AMF inoculants and help farmers determine whether they are appropriate for their system.

Another contributing factor to the poor performance of AMF in agriculture is the quality of

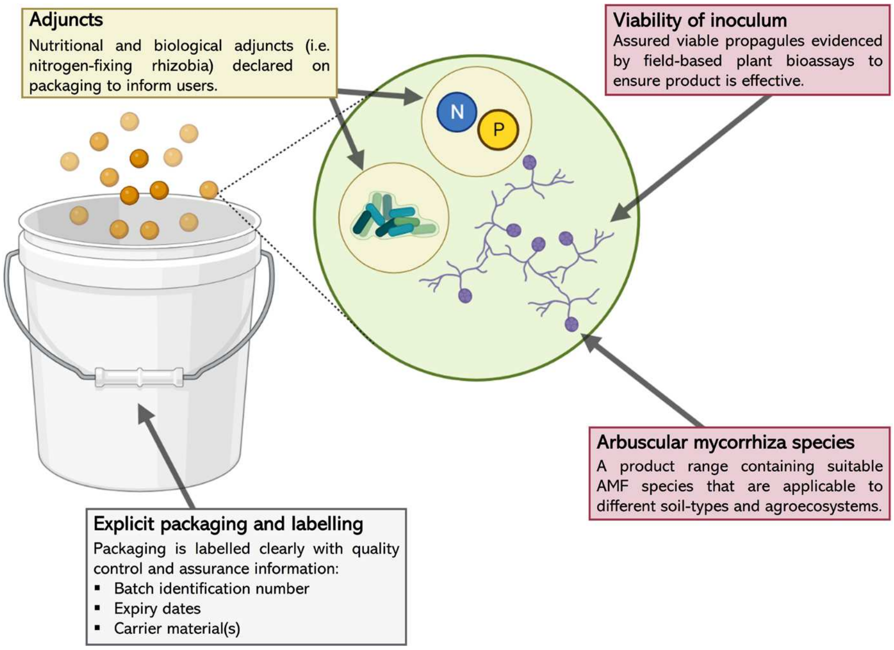

Figure 3. Proposed improvements of commercial AMF-containing inoculants to be improved to ensure their efficacy and reliability. Content and figure adapted from Salomon et al. (2022), which is available under Creative Commons Attribution 4.0 International License.

commercially available inoculants, which have recently come under scrutiny. A study reported that out of 28 products tested, only 16% of products were successful in colonizing plants sufficiently and 35% contained no viable propagules whatsoever. Following these reports, a quality and regulation framework was put forward by an expanded list of authors with the aim to ensure that microbial products contain viable propagules, the absence of pathogens and are packaged with labels explicitly describing their contents and nutrient adjuncts (Figure 3). By improving quality control measures, the benefits of introducing AMF into agricultural soils will be more predictable, which in turn will make their application a more reliable and less environmentally damaging method of improving crop productivity.

In addition, greater scrutiny of production and application of mycorrhizal inoculants will enable more accurate assessments of the sustainability of commercial inoculants. This currently remains unknown as many manufacturers are reluctant to make publicly available the precise components of their products.

The broader benefits of managing agricultural systems for mycorrhizal fungi

The context-dependent nature of host plant benefits derived from AMF and the inconsistency of many commercial inocula have led to doubts regarding the importance of managing agricultural soils to promote AMF. However, managing soils for AMF comes with a wide range of other, non-plant, benefits as mycorrhizal fungi contribute to many ecosystem functions, particularly relevant to agricultural systems. These include improvement in soil structure, promotion of aggregation and greater rates of nutrient cycling. AMF hyphae secrete 'glomalin', an umbrella term for an unidentified combination of glycoproteins that bind soil particles together into aggregates, which can increase soil fertility and water-holding capacity, which ultimately benefits crop plants. Moreover, practices such as intercropping and conservation agriculture that come under the umbrella of 'sustainable farming' do not only help maintain below-ground biodiversity, including mycorrhizal fungi, but also often come with associated benefits such as carbon sequestration, reduced reliance on pesticides and fertilizers, improved water storage capacity and improved soil structure and thus nutrient retention.

It is also important to remember that other than yield quantity, yield quality is also an important factor to consider when producing food. AMF have been shown to increase the biofortification of grains and might also enhance the capacity of storing the harvest. Moreover, if crops are more nutrient-rich, then less quantity might be required which could be achieved with reduced amounts of fertilizers, making the overall process more efficient, more environmentally friendly and more economical. Managing agroecosystems more sustainably will also lead to a positive feedback loop, where soil conditions and crop varieties will better suit mycorrhizal fungi and in turn these fungi will become increasingly beneficial to plants. Rather than trying to make AMF fit into what is commonly viewed as an unsustainable food production system, agricultural systems need to better incorporate wider ecological processes and harness beneficial soil biota, such as AMF.

Future perspectives

Interactions between plants and AMF are complex and have evolved different characteristics over >500 million years. Disentangling the impacts of AMF in agroecosystems is extremely challenging. The findings from lab or glasshouse experiments that focus on single aspects of the symbiosis are useful but do not tell us the full story as, in reality, agricultural systems are complex, replete with multi-trophic interactions and environmental and economic pressures that require careful consideration. Crop yields, while critical for economic and food security, should not be prioritized at the expense of the long-term productivity of agricultural systems. Even if the evidence on mycorrhizal-mediated plant growth responses is sometimes equivocal, the impact of mycorrhizal fungi on broader soil ecosystem performance and resilience should always be considered. In the UK, this is hopefully set to be at least partly captured by the recently launched Environmental Land Management (ELM) scheme which will pay farmers and land managers to deliver, alongside food production, significant and important outcomes for nature and the environment. The intrinsic value of biodiversity has been recognized repeatedly by the United Nations Conventions on Biological Diversity, and despite decades of neglect, this should include below-ground biodiversity and AMF specifically. Overall, the ability of crops to form associations with AMF seems to vary across plant species and environmental conditions. Modern crop cultivars can be less beneficial to fungi and and have unknown consequences for future AMF biodiversity. This underpins the need to carefully consider these broader aspects in breeding efforts to ensure compatibility and function in crop–AMF associations are maintained, especially pertinent under changing future climate conditions. For farmers attempting to shift their agricultural systems to be less environmentally damaging, it is important that suitable and reliable commercial inoculants are available. Practices such as reduced tilling, the use of cover crops and the avoidance of artificial fertilizers are not limited to the promotion of AMF but through the other benefits they offer, they are likely to become more and more important for sustainably enhancing food production. ■

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Katie Field is Professor of Plant-Soil-Processes at the University of Sheffield. Her research spans 500 million years of land plant evolution, focusing on the interactions between plants and the soil around them, including the myriad microorganisms that inhabit the below-ground environment. Katie is interested in the role of soil fungi in plant nutrition in modern and ancient ecosystems, including the role of soil fungi in helping plants get a foothold on land in the Early Devonian. Katie's research also seeks to improve sustainability in agriculture through the potential exploitation of soil microorganisms to improve crop nutrition and reduce chemical inputs. Twitter: @katiefield4 and @Field_lab_UoS. Email: k.j.field@sheffield.ac.uk

