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Arbuscular Mycorrhiza and Sustainable Agriculture

Douglas A. Schaefer[1], Heng Gui[1,2], Peter E. Mortimer[1,2], and Jianchu Xu[1,2*]

[1] *Centre for Mountain Futures (CMF), Kunming Institute of Botany, Chinese Academy of Science, Kunming 650201, Yunnan, China*
[2] *CAS Key Laboratory for Plant Biodiversity and Biogeography of East Asia (KLPB), Kunming Institute of Botany, Chinese Academy of Science, Kunming 650201, Yunnan, China*
* Corresponding author, E-mail: jxu@mail.kib.ac.cn

Abstract

Arbuscular mycorrhizal fungi (AMF) provide benefits to most crop species *via* enhanced nutrient uptake, increased drought and abiotic stress resistance, and reduced effects of pathogens and pests. Much remains unclear regarding the specific mechanisms influencing these processes, and the critical roles of AMF are often overlooked in planning agroecological systems. There is growing consensus, however, around the important roles AMF play in improving plant resilience and crop yield while also enhancing the functioning of soil microbial communities. Heterogeneous practices across all scales complicate the successful integration of AMF in agroecological systems. AMF symbioses with crops are passive, or stimulated by incorporation of crop wastes in soil, soil inoculation with AMF spores, or the planting inoculated of seeds. Here we suggest that AMF can have highest beneficial impacts in areas with low levels of agrochemical inputs. We argue that areas with intensive agrochemical inputs can also be made more sustainable with AMF enhancements.

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INTRODUCTION

Arbuscular mycorrhizal fungi (AMF) belong to the Glomeromycota phylum and engage in symbiotic partnerships with the roots of over 80% of terrestrial plant species. Their hyphae explore large soil volumes, and within plant roots they form arbuscules that exchange chemicals with plant roots. AMF chemical nutrition from soils is compensated by chemical energy supplied by plants to AMF[1]. AMF species have been extensively studied because of their important roles in promoting plant performance and ecosystem services. More specifically, AMF are known to provide benefits to crops in addition to yield enhancement as summarized below (Table 1).

Future agricultural systems will need to provide for a growing human population while also limiting eutrophication of surface waters, mitigating soil erosion, and lowering greenhouse gas emissions. These combined goals are complex and sometimes contradictory. Even so, additions of bio-fertilizers and bio-inoculants can help achieve sustainable agriculture, as these can concurrently deliver multiple ecological benefits. While AMF have entered into mutualistic partnerships with plant roots for about 400 million years, the details of their interactions with crop roots are still not fully understood.

Here we explore AMF in current agricultural systems and the ways in which AMF can make agriculture more sustainable. Section 2 briefly summarizes earlier research on AMF effects on agricultural systems. Gaps in research and applications for agriculture are emphasized. Attesting to the importance of AMF for crop production, approximately 30 meta-analyses have been published, most of which examine the effects of AMF on crop yields. Section 3 addresses how cropping practices and crop species themselves affect AMF symbioses.

Ideal combinations of crops and soil AMF partners could potentially deliver high yields and nutritional quality as well as high conversion of externally applied nutrients into saleable products across all soil/climate combinations. Other benefits could include stronger resistance to herbivory and disease as well as bolstered resilience to both persistent and episodic abiotic stresses. Earlier research summarized in Table 1 illuminates these goals. These AMF-strengthened crops might also be adaptable to agroecological systems with a wide range of agrochemical inputs.

Table 1. Potential effects of AMF on crop nutrition, resilience, stress tolerance, and soil properties.

Effects of AMF on crops and soils	Representative citations
Increased nutrient access by physically and enzymatically expanding the rhizosphere	[2–5]
Increased water use efficiency	[6–8]
Increased stress resistance to drought, salinity and phytotoxic metals	[9–11]
Increased resistance to competition from non-crops (weeds)	[12–15]
Increased soil carbon sequestration	[6,16,17]
Increased soil aggregate formation and reduced soil erosion	[18,19]
Reduced soil nutrient losses in liquid and gas phases	[3,20–22]
Reduced sensitivity to plant pathogens	[23–28]
Reduced sensitivity to herbivory	[29–31]

HOW DO AMF AFFECT CROPS AND SOILS?

The effects of AMF on crops and soils are various and complex. We summarize qualitative effects of AMF on crop nutrition, resilience, stress tolerance, and soil properties (Table 1).

AMF effects on crop yields

Global agriculture is heterogeneous in terms of crops, climate and edaphic patterns, and cropping systems. Uniform yield increases with increased AMF management cannot be expected.

Meta- and other analyses show improved crop yield in response to AMF symbioses[6,28,32–41]. Ryan and Graham argued narrowly (mostly focusing on wheat) that AMF had little effect on crop production[42]. A rebuttal by Rillig et al.[43] to Ryan and Graham[42] provided the original impetus for this overview. We agree with Rillig et al.[43] that Ryan and Graham[42] posed their argument too narrowly, but we further suggest that Rillig et al.[43] understated the extent of potential benefits of AMF for crops, as summarized in Table 1.

Crop-plant phylogeny related to AMF yield effects

We have combined three reviews of AMF yield effects and grouped their results according to phylogenetic relationships among plant families in Fig. 1. Other yield effect studies are not included because data are not readily comparable. Nonetheless, all crop species from those studies are included in Fig. 1, although some effect size ranges may be under-estimated.

The positive and near-neutral effects of AMF inoculations on yield are widely distributed across crop taxa, and show no obvious phylogenetic patterns (Fig. 1). The strongest positive effects are reported for *Panicum virgatum* (switchgrass), a bioenergy crop, suggesting that future AMF research should not be limited to food crops. Compared to other crop

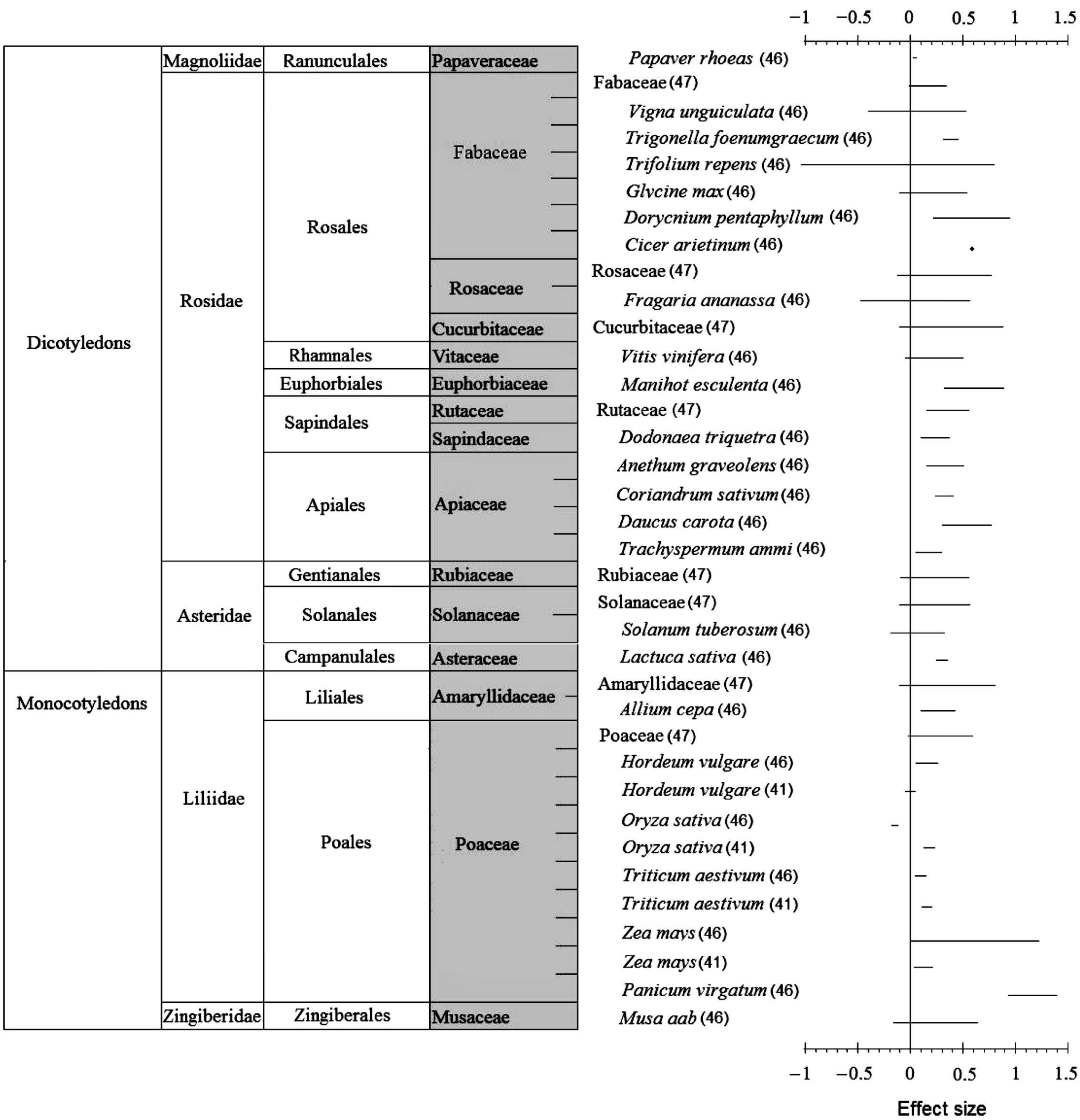

Fig. 1 Crop plant phylogeny related to effect sizes of AMF inoculations on yield in field studies. Data are from references[41,46,47].

phylogenies, another Poales maize (*Zea mays*) also shows large positive effects. This supports the suggestion that grasses benefit from AMF[41], despite their relatively small root diameters. Maize receiving large positive effects from AMF inoculations also contrasts with Ryan and Graham's conclusions mentioned above[42]. Crop yields under both C3 and C4 photosynthetic pathways benefit from AMF symbioses[44], with greater effects on C4 crops, presumably because of higher nutrient demands.

Trifolium repens (white clover) showed the strongest negative effects with AMF inoculations, but this species also presented a wide range of responses (Fig. 1). Across all crop phylogenies, the widest range of yield effects appear in Fabaceae, which is a family characterized by additional symbioses with N-fixing root-associated bacteria. As N-fixing crops are crucial for agricultural sustainability, further research on AMF interactions for crops in this plant family should be prioritized.

Root crops in Euphorbiaceae (*Manihot esculenta*), Apiaceae (*Daucus carota*), and Amaryllidaceae (*Allium cepa*) have positive responses to AMF inoculations, while Solanaceae (*Solanum tuberosum*) mostly has positive responses. No strong phylogenetic differences were observed in these few examples, compared to aboveground harvested crops. Other important root crops are found in families Araceae, Cannaceae, Convolvulaceae, Dioscoreaceae, Lamiaceae and Marantaceae[45]. These crop families are yet to be explored for AMF effects, and accordingly are not presented in Fig. 1. Potential AMF benefits should be further investigated in belowground harvested crops.

Only one perennial crop seems to have been examined (*Vitis vinifera*), which presented neutral to positive yield effects (Fig. 1). The world's two most economically valuable perennial crops are tea (family: Theaceae) and coffee (family: Rubiaceae), and neither has been examined for AMF inoculation effects. Sustainable cultivation of perennial crops could benefit from filling these knowledge gaps.

EFFECTS OF AGRICULTURAL PRACTICES ON AMF SYMBIOSES

Effects of crop rotations, fallow periods and N fixers on AMF performance

As most crops are symbiotic with AMF, we find no reports of any deleterious effects resulting from crop rotations when the different crops in rotation are all symbiotic with AMF[48]. However, there are cases of negative impacts on crop performance when AMF based crop plants are rotated with non-mycorrhizal crops, such as those of Brassicaceae, which are generally not symbiotic with AMF. These non-mycorrhizal crops can constrain AMF performance in rotations and interfere with AMF persistence over time[49]. However, the value of such crops in rotation should be weighed against potential negative impacts that result from these cropping combinations. For example, canola oilseed (*Brassica spp.*) may present considerable local-harvest value, and offset downturns in subsequent productivity of cropping cycles[40].

Nitrogen-fixing crops with root-associated *Rhizobia* bacteria are also associated with AMF, with the latter providing crucial additional phosphorus from soils for this tripartite symbiosis[11,28,35,50–53]. Past studies have also shown that the synergistic effect of the tripartite symbiosis results in greater benefits (improved growth and nutrition) to the host plant than if the host only formed a relationship with one of the symbiotic partners[54,55].

Fallow periods are part of some cropping cycles and are used in conjunction with tillage for weed control, but many studies have shown these practices could exert negative effects on AMF interactions with subsequent negative impacts on crop performance[11,56–59]. Tillage results in an upheaval of soil layers, disrupting established mycelium networks in the soil, upsetting existing microbial communities, and impacting soil density and moisture. All of these factors will impact mycorrhizal communities found within soils, thus potentially influencing crop performance.

Effects of tillage intensity

Effects of crop tillage were an early focus for AMF function[60]. Tillage disrupts extra-radical mycorrhiza, allowing for the possibility that in no-tillage systems, plants may follow old root channels and potentially encounter more AMF propagules than plants growing in tilled soil[61]. AMF present in soils below typical tillage depths, deep-rooted crops, and deep-rooted cover crops can further improve access to AMF benefits[62].

One meta-analysis showed AMF inoculations had the highest effect on AMF colonization of roots, followed by avoidance of nonmycorrhizal plants in crop rotations, shorter fallow times, and reduced soil disturbance, with the smallest effects from mycorrhizal continuous cropping systems[33]. We find no newer study that has more fully isolated AMF functions across crop/soil management practices.

This suggests a need to better assess how external factors influence AMF responses. Less-intensive tillage is a viable strategy for enhancing root colonization by indigenous AMF across soil types and crop species[6]. The same study found that reduced tillage and winter cover cropping increased AMF colonization of summer crop roots by 30%, and also suggested that farmers should seek optimal tillage and cover-crop combinations[6].

Research in under-studied neotropical agroecosystems has recently shown that intensive tillage practices can negatively affect AMF functions[63]. Reduced tillage was more beneficial than crop-residue management in northeast China[64], but this conclusion may not apply across agriculture globally. A comparison of tillage practices over 6 years found AMF spore density and diversity were both reduced by tillage intensity[65]. They further identified AMF as useful indicator species for excessive tillage intensity.

Glyphosate herbicides are typically used in low- and no-tillage systems for weed management[66]. That study found conventional tillage to have greater negative impacts on AMF than zero tillage and glyphosate, but the authors also remarked that glyphosate is detrimental to AMF growth and hinders subsequent AMF recovery.

Effects of inorganic fertilizer inputs and other agrochemicals

Crop varieties were intensively bred in the 1960's Green Revolution for increased yield in response to chemical fertilizer inputs and reduced water supply[67]. Those varieties are also relatively unresponsive to AMF symbioses[28,43,67,68]. The use of fungicides, insecticides, and nematicides negatively affects some aspects of AMF physiology, such as the synthesis of cell-wall chitin[28]. Greater benefits are usually seen in AMF-cultivated plants under organic cropping systems[69] , with lower inorganic nutrient additions, more soil organic matter and organic residues, and limited or no use of other agrochemicals[33].

Increasing future crop production by globally increasing inorganic fertilizer intensity ignores off-site effects and that crop nutrient-use efficiencies never exceed 50%[70]. Green Revolution crop yields have come at substantial environmental costs[67], and any further yield increases must minimize negative effects on ecosystem sustainability[6].

Nutrient access afforded to crops by AMF works in distinct ways. Nitrate ions have high mobility, and are thus present throughout soil layers. Compared to plant roots, AMF hyphae are capable of more thoroughly exploring soil volumes for nutrient extraction. Phosphorous, by contrast, is highly immobile in soils, and mostly occurs in forms not directly accessible by plant roots. AMF and their exoenzymes play pivotal roles in accessing, mobilizing, and transferring these resources in exchange for carbohydrates from plant partners. These symbioses between plant roots and AMF function most efficiently in soil without external chemical inputs. Despite this, there may be a wide range of nutrient-supply rates under which AMF can mitigate nutrient losses from croplands where added fertilizers are not taken into biomass[3].

Comparing (single species 'silver bullet') AMF to inoculations by indigenous AMF

Inoculation of AMF as plant-growth promoters has mostly been conducted using single-species inocula[71]. Those authors also found that inoculation with six locally occurring species gave higher yield responses than did commercial single-species inoculation. Such commercial inoculants (typically *Rhizopus irregularis)* have also been shown to produce few benefits in other studies[58]. Non-local AMF inocula have been considered to be potential environmental risks, and may out-compete local AMF without providing higher plant benefits[43,72]. A lack of consistently higher benefits for plant growth and commercial yields has sparked a debate on how to balance agronomical rewards and potential environmental risks of 'silver-bullet' inocula[43,72]. As such inocula are presently considered potentially beneficial for crops[28], the matter remains unresolved.

In low-input cropping systems, superior results could be obtained if local, fast colonizing AMF inoculants are identified, isolated and cultured for inoculation[73]. Inexpensive and locally produced AMF inoculants have been called for[74]. The possibility of crop-seed coatings containing spores of *Rhizopus irregularis* has also been considered[75].

Composition and diversity of AMF communities have been recognized as key factors in plant responses to colonization and potential received benefits[76]. Thus, it is more likely that indigenous AMF community inoculants will benefit crops in locally distinct climate and edaphic settings. However, intensively managed agricultural systems impose strong filters that limit AMF community assemblages and favor those capable of persisting under high rates of disturbance, long fallow periods, and monocultural plant hosts[76].

Global AMF knowledge to illuminate local utilization

The description of AMF community structures across agroecosystems to identify environmental variables that determine AMF community assemblages has been called for[77]. A large and growing AMF versus crop database is under development[46] that can assist in developing and testing a wide variety of hypotheses. For example, are inoculations with local AMF superior to inoculations with *Rhizopus irregularis* with particular crops or with crops grown in particular areas? Are plant cultivars selected for high availability of soil nutrients less responsive to AMF, and if so, for which cultivars grown where?

Potential effects of future CO_2 on AMF-crop interactions

Families containing major crop species have developed over the most recent 50 million years. During that time, atmospheric concentrations of CO_2 decreased from more than 500 parts per million (ppm) to pre-industrial 280 ppm[78]. During industrialization, CO_2 increased to the current level of 410 ppm and will exceed 500 ppm by mid-century. During the last 50 million years, symbioses between plants and AMF has persisted, although their functional details remain hidden from view.

Studies of AMF-crop symbioses conducted with CO_2 concentrations higher than current levels provide some evidence that crop yields might increase[79−81]. However, contrasting results have also been published[68,82]. These together can be seen as broad evidence that AMF-crop symbioses are resilient against CO_2 increases, but details of AMF benefits to crops (Table 1 and Fig. 1) have not yet been fully explored in this context.

PERSPECTIVE: HOW AMF CAN IMPROVE AGRICULTURAL SUSTAINABILITY

It does not appear that further increases in chemical fertilizer applications can solve the problem of providing enough food for the future. Crop nutrient-use efficiencies are low, and externalities (especially for nitrogen and phosphorous) are high. Exogenous nitrogen additions are energy expensive, and exogenous mineral phosphorous supplies may be limited in the future. Instead, we propose that regionally available AMF should be more fully utilized for crops and soils, but also that global agricultural areas differ in pathways for such management.

Global agricultural N-fertilizer application rates have been mapped[83]. We suggest that in some areas with high rates of fertilizer use, mechanized agriculture and single cropping (e.g., parts of North America and Europe), transitioning to agriculture more dependent an AMF will be slow and incomplete. In other areas with high N-fertilizer application rates (e.g., parts of China and India), crop diversification may be more attractive, and surface-water pollution reduction can be achieved with reducing fertilizer loading. Some of these areas may transition to producing crops more dependent on AMF, realizing sustainability benefits and offer technological leadership. Areas with relatively low N-fertilizer application rates (e.g., Africa and South America) currently grow crops at lower rates of productivity. Increasing fertilizer application rates in these areas would increase costs, and local actors may conclude that optimizing crops and AMF interactions may do more to improve benefit/cost ratios. These areas are probably less likely to invest in chemical herbicides and pesticides, and may conclude that improved AMF-crop associations are effective and sustainable.

The Green Revolution developed crop varieties that relied upon large agrochemical inputs. These varieties and their chemical management practices are not ideal for sustainable use and to meet the need for further increasing agricultural production. The clear goal for intensification of sustainable agriculture is to provide better food production without degrading other aspects of global ecosystems. This overview shows that AMF-crop interactions are a potential way forward for achieving this goal. More in-depth research is needed here, particularly studies that focus on local crops, local cropping practices, and projected future environmental conditions.

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Conflict of interest

The authors declare that they have no conflict of interest.

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