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Arbuscular mycorrhizal networks—A climate-smart blueprint for agriculture

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ABSTRACT

The arbuscular mycorrhizal (AM) fungal symbiosis offers a transformative solution to mitigate agroecosystem challenges linked to the excessive use of synthetic chemicals. However, the role of AM–plant communication in response to anthropogenic activities and hyphal network functionality remains poorly understood. Here, we reposition AM fungal hyphosphere networks as a keystone ecological infrastructure for sustainable agroecosystems. Drawing on a synthesis of thousands of global experimental studies, we highlight the primary environmental functions of AM fungus–plant communication: enhancing agroecosystem resilience by buffering crops against diverse biotic and abiotic stressors through molecular signaling and physiological modulation, mediating energy transfer via small-RNA-mediated cross-kingdom interactions, facilitating hydraulic redistribution within the soil profile through hyphospheric networks, and optimizing root architecture via effective colonization for improved nutrient acquisition. Certain anthropogenic practices—such as soil disturbance, non-mycorrhizal crop monoculture, and fungicide application—can disrupt AM hyphal networks; however, these impacts can be minimized through improved farming practices, such as cropping diversification with legumes and AM fungus–compatible crops, AM-responsive plant genotypes, effective AM fungal inoculation, and microbial consortium amendments. Integrating insights into AM fungal mechanisms with anthropogenic practices and policy support is essential to scaling AM benefits across ecoregions. Harnessing AM fungal functionality can increase nutrient use efficiency, reduce reliance on chemical inputs, and enhance ecosystem productivity, offering a microbe-centered blueprint to support the United Nations' sustainability goals.

Key words: biofertilizer, hyphosphere, cropping diversification, agroecosystem resilience, cross-kingdom communication, soil health

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INTRODUCTION

Global agriculture is confronting a formidable triple imperative: sustaining escalating demands for food, feed, and fiber production; mitigating climate disruptions; and improving soil health (Anonymous, 2024; Wang et al., 2025c). Twentieth-century industrialized agriculture achieved unprecedented yield increases through deployment of synthetic agrochemicals (Pretty, 2018), but recent data reveal stagnating productivity trajectories (Gerber et al., 2024). Current paradigms necessitate disproportionate chemical inputs for marginal yield gains, thereby inflating production costs (Gu et al., 2023) and perpetuating ecological degradation (Tian et al., 2020)—manifested as terrestrial pollution (Guo et al., 2020), pedogenic acidification (Marris, 2022), and biodiversity collapse (Cabernard et al., 2024). Such chemical intensification destabilizes the plant–soil–microbiome equilibrium, nullifying the ecological services of soil microbial consortia (Banerjee et al., 2019). Furthermore, global agrochemical manufacturing alone emits approximately 300–400 million tons of CO_2 annually, exacerbating climate feedback loops. These realities urgently necessitate the development of sustainable alternatives that decouple agricultural productivity from synthetic chemical inputs while minimizing environmental externalities—a defining challenge for 21st-century agroecosystem management.

An alternative approach to traditional agrochemical use involves harnessing the functional capabilities of soil microbial communities, such as the arbuscular mycorrhizal (AM) fungal symbiosis (Salvioli di Fossalunga and Bonfante, 2023), one of the most common plant–microbe symbioses, which occurs in about 80% of vascular plant families (Brundrett and Tedersoo, 2018). AM fungi colonize plant roots through germinating spores, forming hyphal branches and establishing mycelial intercellular hyphae (Figure 1). This colonization involves asymbiotic, pre-symbiotic, and symbiotic stages (Choi et al., 2018). The extraradical AM fungal mycelium provides nutrients to the host. In return, host plants provide carbon (C) sources, mainly fatty acids (Luginbuehl et al., 2017), for AM fungal survival and growth, thus sustaining colonization (Jiang et al., 2017). The mutualistic symbiosis grows into the soil, creating AM hyphospheric networks (i.e., networks in which AM fungi release hyphal compounds into the soil to orchestrate the hyphosphere colonized by a diversity of microbes). These networks enable plant roots to access a larger resource area in the soil (Rillig et al., 2025). Complex mycelial hyphospheric networks bridge soil gaps, as well as increase antioxidant enzyme activities and facilitate nutrient exchange beyond colonized roots (Callahan, 2025).

In addition to nutrient uptake, hyphospheric networks provide various ecological services (Figure 2), systemically inducing physiochemical changes in colonized plants that protect against various abiotic and biotic stressors and soil contaminants, such as heavy metals, by activating immune responses or secreting functional enzymes that modify host-plant cell functions (Wanke et al., 2023). The magnitude of these ecological functions is shaped by environmental filtering, spatial variability, stochasticity, and niche breadth (Liu et al., 2024b). In cultivated ecosystems, multiple AM fungal species and microbes can colonize plants simultaneously, and a single plant genotypic species can connect multiple AM fungal species to form distinct hyphospheric networks (Liu et al., 2024a). Thereby, antagonistic interactions between host plants and AM fungi or between AM fungi and other microbes may occur under some specific conditions. Also, host-to-host interactions may alter the abundance of fungal partners, potentially hindering extraradical network growth (Engelmoer and Kiers, 2015).

Despite the potential of using AM fungal symbiosis as an alternative or biofertilizer to substitute for agrochemicals, the mechanisms that govern the soil–plant–microbiome continuum are poorly understood. Nutrient translocation from the AM fungus–induced hyphospheric network to plant roots in response to anthropogenic practices, such as soil disturbance via tillage and crop rotation, has not been well characterized. Recent efforts to manipulate the rhizosphere or engineer the hyphosphere have aimed to enhance biofertilizer-modulated soil health (Wang et al., 2024b). Still, the effectiveness of this approach under diverse soil–climate conditions is uncertain. Moreover, commercial AM fungal inoculants have shown low efficacy or inconsistent results. A recent (2024) meta-analysis synthesizing the results of experiments across four continents showed that commercial mycorrhizal products had about 10% efficacy owing to poor product quality (Koziol et al., 2024). By contrast, meta-analyses integrating hundreds of publications (Wojciechowski et al., 2023; Ge et al., 2025) revealed that cover-cropping systems enhanced AM fungal colonization, spore abundance, and extraradical biomass by 34%–55% and that intercropping increased these AM benefits by 20%–25%. However, crop rotation reduced the AM fungal richness of plant roots by 43%. These diverse findings demonstrate that anthropogenic activities and methods of handling and applying AM products to fields play vital roles in AM fungal survival, functionality, and ecosystem services. We must address unanswered questions regarding the effective use of the AM fungal symbiosis in real-world agriculture by shifting our focus to the urgency of harnessing the potential of AM fungi in agriculture. For instance, when should AM inoculants be applied in the field to maintain their viability? How do soil moisture and temperature affect the efficacy of AM inoculants? Do they merely colonize plant roots without functional benefits? How do cropping systems (Ge et al., 2025), cultivar choices (Oladele et al., 2025), or plant diversity (Trivedi et al., 2020) affect AM symbiotic function in different soils?

In this study, we aimed to (1) explore the primary roles of AM fungus–dominated hyphospheric networks in improving agroecosystem services and functions, and the relationship between host crop diversity and AM fungal diversity in shaping plant–soil–microbiome associations, (2) assess AM fungi as biofertilizers to enhance nutrient use and productivity in agroecosystems, and (3) provide evidence-based recommendations to optimize AM fungal functioning by improving anthropogenic practices and adopting innovative technology for soil and crop management.

MAIN ROLES OF AM FUNGAL HYPHOSPHERIC NETWORKS

Buffering responses to multiple global-change factors

The impending environmental disturbances and pollutants resulting from global climate change are expected to intensify, posing

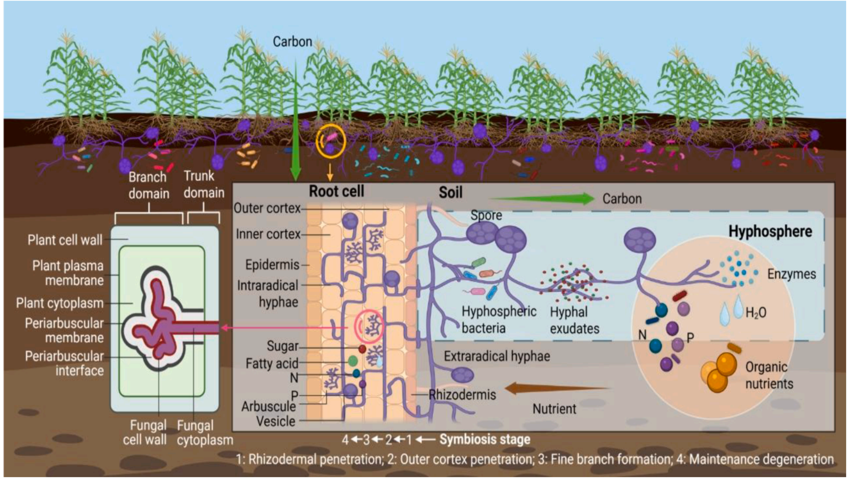

Figure 1. Schematic illustration depicting AM fungal colonization and symbiosis formation.

AM fungi initially colonize plant roots through germinating spores, forming hyphal branches and establishing intercellular hyphae. This colonization involves asymbiotic, pre-symbiotic, and symbiotic stages (steps). During the asymbiotic stage, AMF spores germinate and initiate mycelia; during the pre-symbiotic stage, chemotropism activates physical contact with roots, and hyphopodia form. During the symbiosis stage, the development of extraradical and intraradical mycelium leads to symbiosis formation and root colonization. An extraradical mycelium provides nutrients to the host, and in return, the host offers C sources for AM fungal survival and growth. This chart was drawn using materials supplied by BioRender (https://www.biorender.com).

significant challenges to soil–water–organism interactions (Wang et al., 2025b; Callahan, 2025). Leveraging the symbiotic relationship between plants and AM fungi offers a promising solution to mitigate these challenges. A 2023 meta-analysis synthesizing 360 published studies across 181 plant species showed that AM fungi protect plants from multiple global-change factors (Tang et al., 2023). In particular, AM symbioses can ameliorate plant damage from drought (Tang et al., 2023) and high-temperature stress (Mathur and Jajoo, 2020; Zaman et al., 2024). The biophysical mechanisms associated with this amelioration are not well documented. Still, we find that the positive effects on reducing these climate-change-induced stresses are closely related to increases in aboveground parameters such as leaf number, plant biomass, and net photosynthesis (Tereucán et al., 2021; Zaman et al., 2024); belowground parameters such as nutrient content and moisture transfer (Tang et al., 2023); alteration in photosystem II heterogeneity in the context of AM fungi and high-temperature stress (Mathur and Jajoo, 2020); and maintenance of the levels of reactive oxygen species, by-products of metabolic reactions (Shankar et al., 2024) that are involved in maintaining biochemical and cellular processes including the cell cycle, programmed cell death, growth and development, hormonal signaling, and biotic and abiotic stress responses (Khatri and Rathore, 2022).

Another broadly recognized benefit of AM hyphospheric networking is "phytoremediation"—an emerging ecosustainable approach to alleviating soil pollution—which enhances nutrient acquisition under adverse conditions (Riaz et al., 2021; Lounès-Hadj Sahraoui et al., 2022). The mechanisms of phytoremediation include (1) increasing concentrations of hormones such as indole acetic acid, indole butyric acid, gibberellic acid, and abscisic acid along the hyphosphere (Parniske, 2008) to regulate physiological responses and gene expression in the AM-colonized host plant; (2) producing additional glucose, soluble proteins, and antioxidant enzymes (Zayova et al., 2018) to alleviate environmental stresses (Chandrasekaran and Paramasivan, 2022); and (3) decreasing glutathione levels and suppressing excessive reactive oxygen species (e.g., hydrogen peroxide) to mitigate oxidative membrane damage (Khoulati et al., 2025). Another broadly recognized benefit of AM hyphospheric networking is "detoxification"—a practical biological approach to protecting plants against arsenic contamination, restricting the uptake of harmful heavy metals from the rhizosphere (Pan et al., 2024), and limiting their translocation from roots to aerial tissues (Riaz et al., 2021). AM-colonized roots also mobilize immovable nutrients such as Cu and Zn within the rhizosphere, reducing their toxicity to host plants (Lu et al., 2024). As a result, AM fungal inoculation can reduce the use of synthetic chemical fertilizers while increasing crop productivity. Meta-analyses have revealed that AM inoculation reduces fertilizer costs by 20%–40% in smallholder maize farms in sub-Saharan Africa while improving yield stability under climate extremes. A global meta-analysis synthesizing the findings of hundreds of studies revealed that AM fungal inoculation increased the yields of field-grown cereal crops by an average of 16% (Zhang et al., 2019b), primarily by increasing N and P acquisition from the soil. This cost–benefit asymmetry underscores the potential of AM fungi to democratize access to sustainable practices. AM fungus–mediated stress resilience is particularly critical for women-led farms in arid regions, where labor-intensive agrochemical management exacerbates gender disparities.

However, the functionality of AM mycorrhizal networking in influencing crop productivity is highly contingent, regulated by interactions among fungal species, host-plant health, and environmental factors. For instance, *Plantago lanceolata* L. plants colonized by *Glomus hoi* or *Rhizophagus intraradices* (formerly *Glomus intraradices*) display temperature-dependent growth responses (Alster et al., 2021). As global climate change progresses, fungal biodiversity may become increasingly critical, as functional traits diverge along phylogenetic lineages. How AM fungi interact with diverse microorganism communities is still unclear. Significant knowledge gaps persist regarding the effects of climatic factor dynamics on the soil–AM fungus–plant continuum in diverse agroecosystems.

Interactions of plant diversity with AM fungal diversity

The interactions between crop diversity and AM fungal diversity can influence the functioning and services of agroecosystems. A suite of ecological, edaphic, and anthropogenic factors govern

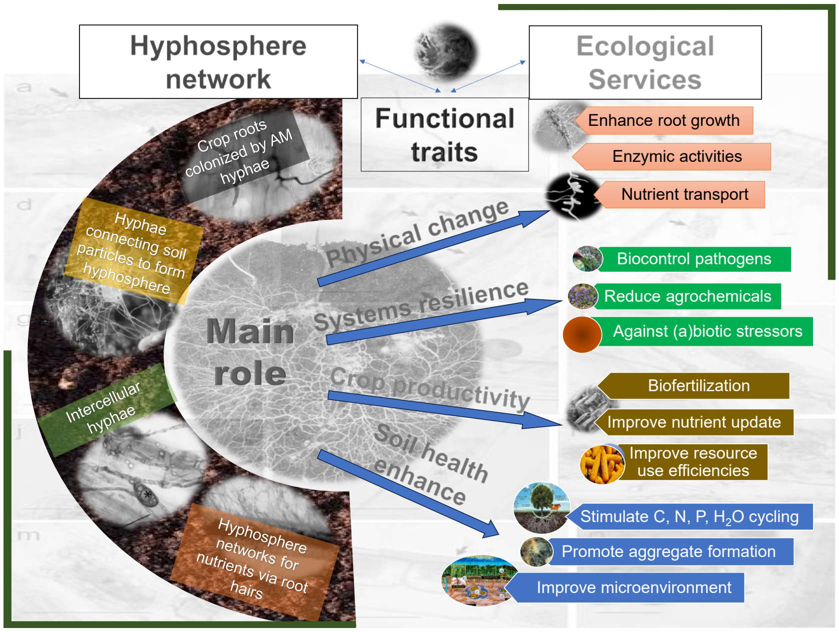

Figure 2. The main functions of AM hyphospheric networking in cultivated systems.
The hyphospheric network is characterized by colonization of crop roots by AM hyphae that connect soil particles to form a hyphospheric network, which recruits beneficial microbiomes and translocates nutrients via root hairs. The AM hyphospheric network has four main functions in cultivated ecosystems: (1) inducing changes in plant physiochemical traits, (2) enhancing the resilience of cropping systems by alleviating abiotic and biotic stressors, (3) increasing crop productivity through biofertilization effects and improved nutrient exchange and use efficiencies, and (4) enhancing soil health by forming soil aggregates that stabilize soil carbon and interacting with other microbes to influence soil structure and fertility. Several indicators reflect each of the four main functions.

the outcomes of these interactions, mediated through mechanisms that span from molecular signaling to ecosystem dynamics (Guzman et al., 2021). First, crop functional diversity directly shapes AM fungal communities by altering root exudate profiles, which act as a chemical signal for fungal symbionts. Diverse crop assemblages enhance niche partitioning, fostering distinct AM fungal taxa adapted to specific root chemistries and nutrient demands (Town et al., 2022). Functional traits such as root architecture (e.g., fibrous vs. taproot systems) further modulate fungal colonization strategies (Zhang et al., 2025). Second, diversified planting induces diversity in soil characteristics such as pH, texture, and organic carbon content that strongly filter AM fungal communities. For instance, acidic soils favor *Glomus* taxa, whereas pH-neutral soils support *Claroideoglomus*. Resource availability (e.g., soil C:N ratios) modulates fungal functional guilds, such as nutrient-foraging vs. stress-tolerant AM taxa. Third, the diversity of mycorrhizal fungal species significantly influences host-plant community structure and development, as AM fungal richness affects soil properties, a legacy effect on plant biodiversity (Zárate Martínez et al., 2024).

Furthermore, AM fungi may have asexual or sexual life cycles, leading to genetic complexity and dynamism within the intimate plant–AM fungus interactions (Kokkoris et al., 2021). Systems with low AM fungal species richness or shifts in AM fungal composition can drive substantial fluctuations in plant species composition and community dynamics. For instance, in *Festuca arundinacea* prairie mesocosms, increased AM fungal richness enhanced host-plant diversity and productivity (Vogelsang et al., 2006). AM fungal dynamics can act as a potential switch point to determine the trajectory of the plant community during succession (Koziol and Bever, 2019). Divergent life-history strategies among AM fungi enable hyphae to acquire nutrients across varying spatial scales, while seasonal and temporal dynamics shape AM fungal community competition with other microbes (Valentin et al., 2023). Mycorrhizal fungi facilitate niche differentiation through spatial, temporal, and evolutionary processes, forming distinct AM functional groups. Increasing the AM fungal functional group enhances coexistence capacity and species diversity by integrating a broader range of plant functional traits. The robustness of plant–AM fungal linkages arises from co-responsiveness, though unexpected antagonisms or altered associations between the two may occur under some conditions (Sendek et al., 2019).

In cultivated soils, the co-responsiveness is jointly determined by plant community composition and AM fungal richness. Plant productivity responds more strongly to AM fungal identity (e.g., species-specific effects) than AM fungal diversity per se (species composition, mixing). The interaction between AM fungal diversity and plant genotype diversity is modulated by soil nutrient availability and climate factors. Three mechanisms—selection effects, complementarity effects, and intra- and interspecies interactions—govern the outcome of crop diversity and AM fungal diversity in influencing agroecosystem functions and services.

The selection effect refers to competition and coordination between AM fungi and host plants. In the diverse-functioning context, the selection effect measures the probability that plant communities with the genotypes of dominant traits disproportionately drive ecosystem processes and productivity. A "host filtering" effect may occur, in which plant traits (e.g., root exudates, phylogeny) selectively recruit or exclude specific microbial taxa. For example, the Brassicaceae family is unique because it does not foster functional symbiosis with AM. This family is also notable for possessing glucosinolates, a class of secondary metabolites that function predominantly in plant defense. Isothiocyanates, the toxic degradation products of glucosinolates, particularly indolic and benzenic glucosinolates, are known to be involved in the inhibition of AM (Sharma et al., 2023). In addition, phylogenetically conserved crops (e.g., monocots) share ancestral traits that favor associations with specific AM fungal lineages (e.g., *Glomeraceae*), reflecting evolutionary coadaptation. Non-hosts, like brassicas, lost mycorrhizal associations during their evolution and act as "ecological interrupters" in agroecosystems. Furthermore, in the face of abiotic stressors such as soil pollution, nutrient deficiency, and elevated CO_2 (Supplemental Table 1), coexisting AM fungal species may adapt morphologically, biochemically, or molecularly to survive. Fast-adapting AM fungal species can dominate resource competition, outcompeting coexisting slow-growing taxa.

The complementarity effect arises from niche differentiation between AM fungi and plant genotypes, in which the presence of one partner enhances the survival and growth of the other, fostering mutualistic fungal associations. Nutrient exchange can also occur between neighboring plants via between-plant complementarity in root exudates. Loss of carbon inputs into AM fungal hyphae from one plant can be ameliorated through inputs of a neighbor, based on an unequal trade for symbiosis (Durant et al., 2023). In grasslands, fungal diversity mediates rapid incorporation of plant-derived carbon into ecosystem cycling, aiding plant recovery from anthropogenic soil disturbance (De Deyn et al., 2011). Facultative mycorrhizal plants (e.g., *Brassica* spp. and *Arabidopsis*) lack evolutionary adaptations to regulate fungal colonization, making them vulnerable to parasitic carbon extraction (Cosme et al., 2018). Functional complementarity, driven by diverse AM fungal traits, promotes resource use efficiency across spatiotemporal gradients, stabilizing AM species coexistence and enhancing agroecosystem productivity.

Intra- and interspecies interactions highlight the complexity of AM fungus–plant relationships. In plant–fungal feedback loops, plants selectively recruit AM fungi through root exudates (e.g., strigolactones), creating positive feedback loops, with diverse crops sustaining diverse fungal consortia. This "partner choice" mechanism is modulated by defense signaling. In cultivated cropping systems, plant genotypes shape AM fungal communities by hosting different AM fungal taxon identities and richness (Lekberg and Waller, 2016). Flowering plant genotypes typically exude strigolactones into the rhizosphere to promote AM fungal symbioses and alter AM fungal community structure. Plant root density (Zhang et al., 2022b) or the ability to resist disturbance (e.g., invasion) (Wang et al., 2025a) plays a critical role in shaping the functioning of the AM community. However, AM fungi can sometimes exhibit "parasitic interactions," i.e., AM fungi gain benefits that come at the expense of the plant host, under specific ecological and edaphic conditions, deviating from their classic mutualistic role (Kaur et al., 2022; Voller et al., 2024; Lewe et al., 2025). This shift occurs when the costs of maintaining the symbiosis (e.g., carbon allocation to fungi) outweigh the benefits (e.g., nutrient acquisition). When soil P or N levels are abundant, plants reduce carbon allocation to AM fungi because fungal-mediated nutrient uptake becomes redundant (Jiang et al., 2018). However, AM fungi may continue to exploit host carbon without reciprocating benefits, leading to asymmetric resource exchange. Parasitic interactions may also occur when AM fungi associate with non-mycorrhizal plants to acquire carbon without reciprocating benefits (Cosme et al., 2018). The outcomes of the dual interactive diversity for agroecosystem functions and services depend on nutrient stoichiometry between the two partners. The capacity of fungal mycelia to enrich hyphospheric nutrients may promote, have no effect, or inhibit host-plant growth (Romero et al., 2023).

Activating signals against (a)biotic stressors

AM fungi are critical for activating plant defense systems—a key mechanism for stress resilience in agriculture. Crop plants face diverse stressors, including physical damage, herbivory, drought, temperature extremes, heavy metals, salinity, and microplastics (summarized in Supplemental Table 1). AM fungal mycelia act as signaling conduits, triggering biochemical defenses by releasing volatile organic compounds to deter herbivores. AM fungi can concurrently colonize plants while activating signals against pathogens, enhancing plant disease resistance through immune activation. Meta-analyses of 130 comparisons derived from 69 published studies show that AM fungal inoculation reduces necrotrophic diseases, an effect driven by AM fungal regulation of jasmonic acid, salicylic acid signaling pathways, and secondary chemicals (Liu et al., 2024a). Some enzymes regulate signaling pathways against pathogens, such as blight disease in crops, acting as biocontrol agents (summarized in Supplemental Tables 1 and 2). For example, *Rhizophagus* spp. (Glomeraceae) induce antioxidative enzyme activities to mitigate oxidative stress (Wang et al., 2022), and effector proteins secreted by AM fungi suppress pathogenic agents (Aparicio Chacon et al., 2023). The coinoculation of *G. intraradices* and *Trichoderma harzianum* increases P uptake in vegetable crops while suppressing *Fusarium oxysporum*–induced wilt (Martínez-Medina et al., 2011). When a stressor attacks plants whose neighboring plants have not yet been attacked, AM fungi can transmit stress signals from the damaged to the healthy plants, upregulating defense-related genes (e.g., *PAL*, *PR-1b*, *ERF3*, and *LOX*) to minimize damage to the whole plant community (Alaux et al., 2020). This biocontrol mechanism demonstrates the role of AM fungi in systemic pathogen resistance. Furthermore, AM fungal hyphospheric networks can act as a bioameliorant (Chen et al., 2023) that reduces elements toxic to crop plants, a remediator (Banerjee et al., 2025) that improves nutrient cycling in mining-affected areas, and a soil reclaimant (Navnage et al., 2024) that alleviates soil contaminants such as heavy metals (summarized in Supplemental Table 3).

Optimizing P supply is a significant challenge in crop production, given the limited availability of rock phosphate and the poor mobility of P in soils. AM fungal inoculation enhances P uptake by releasing active signals when P deficiency occurs. Cotton (*Gossypium hirsutum* L.) colonized by *Rhizophagus irregularis* CD1 exhibited upregulated P-transporter gene expression (Gao et al., 2020), leading to a 29% yield increase via enhanced chlorophyll content and photosynthesis (Al-Arjani et al., 2020). Increased P availability boosts photosynthetic capacity by enhancing light-dependent reactions, Calvin cycle enzymes, ATP and NADPH synthesis, and nucleic acid production (Chandrasekaran et al., 2019). In addition to providing timely signaling for plants in P-deficient situations, AM fungi improve the acquisition of other nutrients, such as K, magnesium (Mg), and calcium (Ca). In tomato (*Solanum lycopersicum* L.), AM fungi regulate zinc (Zn) uptake in two ways: enhancing Zn absorption below a critical threshold, while restricting Zn translocation to shoots at higher Zn concentrations (Bhantana et al., 2021). In addition, AM fungi can modulate phytohormones like cytokinins as a signal (Cosme et al., 2016), promoting chloroplast development and delaying senescence.

AM fungi mediate carbon decomposers

AM hyphae play a key role in soil food webs, regulating carbon-cycle processes such as assimilation, decomposition, and stabilization of organic matter (Wu et al., 2022c). Host plants and AM fungi can influence one another across spatial and temporal scales, in which AM mycelia extend into soil to access organic matter, linking carbon cycles through shoot-to-root carbon transport and driving biogeochemical processes (Hawkins et al., 2023). In this review, we find that the biochemical pathways underpinning AM fungus–driven carbon dynamics include, but are not limited to, the following:

1. AM fungi engage in cross-kingdom interplay with soil microbiomes, interfacing with the organic–mineral matrix to catalyze redox-driven transformations of organic matter (Kleber et al., 2021).
2. Hyphal exudation of low-molecular-weight metabolites (e.g., fructose) and high-complexity biomolecules (e.g., glycoproteins) directly primes carbon fluxes along the hyphosphere "highway" (Zhang et al., 2022a).
3. AM fungus–derived exuded surfactants induce the formation of soil aggregates (Baumert et al., 2018), sequestering labile carbon into stabilized microhabitats (Zhang et al., 2020). In this function, AM fungal networking mainly influences soils that harbor microaggregates (Totsche et al., 2018).
4. AM fungi orchestrate hyphospheric enzymatic cascades (Zhang et al., 2022a), recalibrating organic matter decomposition kinetics and facilitating the neo-synthesis of recalcitrant C compounds (Tanaka et al., 2022; Wu et al., 2023).
5. Mycelial hydrotropism synergizes with hydraulic gradients to expedite nutrient mobilization and C translocation.

Rising atmospheric CO_2 levels are anticipated to disrupt global carbon cycling dynamics. First, elevated CO_2 can enhance photosynthetic carbon fixation, which may increase rhizodeposition and alter belowground carbon allocation processes. In this context, AM fungal hyphae function as critical conduits, transporting plant-derived carbon into the hyphosphere to strengthen soil organic carbon (SOC) storage. Concurrently, climate-driven selection pressures are most likely to promote the development of novel AM-associated microbial communities specialized in modulating carbon cycling. However, the interaction between human activities (e.g., land-use practices and fertilization) and AM fungal roles in climate–carbon feedbacks remains a key knowledge gap that requires further investigation. For instance, meta-analyses of 97 global trials revealed that AM fungi negatively influence soil carbon storage by promoting the "priming effect" (Choreno-Parra and Treseder, 2024), in which AM hyphae absorb plant-derived carbohydrates and lipids via signaling feedback. These results indicate that AM hyphospheric networks can neutrally or negatively affect host-plant community functioning, and anthropogenic activities may govern the outcomes.

AM fungal hyphospheric networks govern hydraulic redistribution

The AM fungal hyphospheric network constitutes a hydraulic lifeline in water-limited agroecosystems, with its role in plant–water relations attaining paramount importance in xeric edaphic environments. In intercropping matrices, AM hyphae mediate hydraulic redistribution from deep-rooted taxa (e.g., *Cajanus cajan* L.) to shallow-rooted cohorts (e.g., *Eleusine coracana*) through hyphosphere-mediated root architectural plasticity (Singh et al., 2019). In contrast to conventional soil hydrology models that emphasize matric-bound water flow, an AM hyphospheric network enables direct apoplastic water transfer via interconnected hyphae (Pauwels et al., 2023). Diurnal hydraulic reversibility manifests in arid zones, with transpirational water flux dominating daylight hours and nocturnal hydraulic reflux replenishing fungal reservoirs in soils (Barto et al., 2012). Hyphal surface hydrophilicity facilitates gradient-driven hydraulic redistribution, culminating in interspecific water subsidization—a process termed "mycohydrologic bioirrigation" (Singh et al., 2019).

A compartmentalized microcosm trial using isotopic tracers revealed that an AM hyphospheric network enabled hydraulic lift from pigeon pea (*C. cajan*) to finger millet (*E. coracana*), with deuterium-labeled water transfer enhancing recipient survival by 38% under acute drought stress (Singh et al., 2019). Alternate wetting–drying irrigation regimens that synergize with AM symbiosis enhance crop production in rice (*Oryza sativa* L.) via AM-induced upregulation of aquaporin expression and osmotic adjustment mechanisms to bolster drought resilience (Das et al., 2022). These adaptations position the AM hyphospheric network as a critical amplifier of agricultural water productivity amid climate-driven aridification.

AM hyphospheric networks regulate nutrient cycling

AM fungal hyphospheric networks can act as biogeochemical engineers, orchestrating cross-kingdom nutrient economies (Duan et al., 2024). Mycorrhizal plants that form a symbiosis with AM fungi experience the top-down carbon flow and the bottom-up mineral flow in this continuum (Wang et al., 2024a). Plants take up nutrients from the soil through two pathways: the root pathway via root epidermal cells and root hairs, and the mycorrhizal pathway via the extraradical hyphae. AM-induced symbioses produce exudates to recruit the microbiome to the rhizosphere and hyphosphere, governing plant nutrient uptake efficiency (Zhang et al., 2022a). The recruited microbiomes along the hyphosphere produce enzymes, stimulating the mineralization of organic nutrient forms. Furthermore, hyphospheric bacteria colonize the soil that surrounds the extraradical AM fungal hyphae (Wang et al., 2024a). AM fungus–bacterium cross-kingdom interactions influence the biogeochemical cycling of nutrients (Duan et al., 2024), enhancing nutrient availability for the interacting organisms (including the host plant, AM fungi, and hyphosphere bacteria) and helping to support the whole ecosystem (Zhang et al., 2022a).

In a complex cultivated ecosystem, anthropogenic practices can influence the outcome of the interactive functions. Legume–cereal intercropping can exemplify this symbiosis, in which AM mycelia channel fixed N from *Rhizobium*-inoculated legumes (e.g., *Vigna radiata*) to cereals (e.g., *O. sativa*), circumventing soil N immobilization (Li et al., 2009). Isotopic fractionation studies using ^{15}N tracing techniques have quantified N transfer efficiencies ranging from 5% to 17% in rice–mung bean (*V. radiata* L.) intercropping systems, together with 65% and 57% enhancements in P acquisition by legumes and cereals, respectively (Li et al., 2009). This tripartite synergy—encompassing AM fungi, N-fixing rhizobia, and host plants—redefines traditional plant–microbe nutrient competition paradigms.

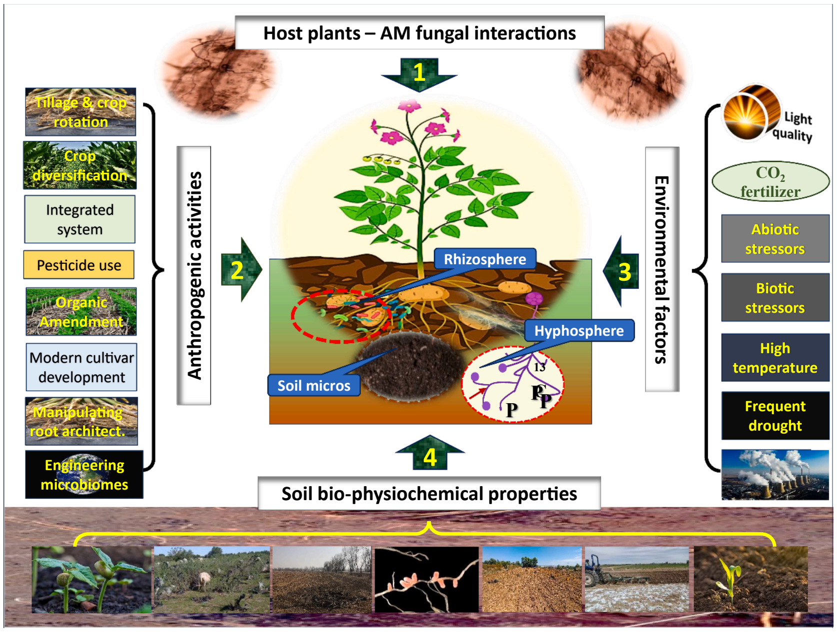

Figure 3. Main factors affecting AM hyphospheric networks in agroecosystems.
(1) Host plant–AM fungus interactions that determine bilateral nutrient exchange; (2) many anthropogenic activities, including but not limited to tillage and crop rotation, crop diversification, integrated management practices, pesticide use, organic amendments, cultivar characteristics, and efforts to modify root architecture and engineer soil microbiomes; (3) environmental factors, such as light quality and CO_2 fertilization, that influence plant photosynthesis and carbon translocation to AM hyphae, and climate-change-induced (a)biotic stressors; and (4) soil properties, such as soil temperature and moisture, that affect AM fungus survival and hyphosphere growth; soil aggregates and structure, which facilitate AM hyphae formation; and soil biological properties, which affect the ability of AM fungi to recruit or interact with other microbiomes to promote nutrient transfer from the hyphosphere to plant roots.

Furthermore, metagenomic correlations between hyphal density and *nosZ* gene abundance underscore the role of AM fungi in mitigating N_2O emissions via enzymatic stimulation of N_2O reductase in denitrifying microbiomes (Zhao et al., 2021). A negative relationship between soil P availability and the rate of AM fungal root colonization often occurs because the extra P "mined" from the soil P "bank" made available to host plants reduces AM fungal colonization. However, the inhibitory effect of soil P on AM symbiosis and function varies among AM fungal species and plant genotypes (Qin et al., 2020). Overcoming the inhibitory effect of high P doses on AM colonization and its functioning may involve identifying compatible plant genotypes and genotype-specific AM adaptations for high-P soils (Smith et al., 2004). This suggests significant potential to exploit AM-assisted nutrient pathways even in high-P agricultural soils.

ANTHROPOGENIC PRACTICES THAT INFLUENCE AM FUNCTIONS

Anthropogenic practices that disrupt AM fungal functions

Anthropogenic activities exert profound influences on root colonization, symbiosis formation, and function of the AM fungi's hyphospheric network (Figure 3). Here we highlight some of the major anthropogenic activities that may adversely affect AM fungal functions in agroecosystems.

(1) Soil disturbance, like tillage, interrupts AM hyphosphere networks (Kabir, 2005) (Figure 3). First, mechanical soil disturbance directly severs the extensive extraradical hyphae of AM fungi. These hyphae form interconnected networks that extend beyond plant roots to access nutrients and water in the soil. Breaking these hyphae reduces their ability to transport nutrients and support symbiotic relationships with plants and soil microbes. Second, tillage disrupts soil aggregates and pore spaces that are critical habitats for AM fungi and their associated hyphospheric microbes. The loss of stable microhabitats reduces hyphal survival and limits the formation of water films on hyphal surfaces, which are a key pathway for bacterial mobility (e.g., phosphate-solubilizing bacteria) along fungal "highways." This disruption impairs nutrient cycling and microbial interactions in the hyphosphere (Banerjee et al., 2019). Third, mechanical tillage damages crop roots, causing plant stress that reduces carbon allocation to fungal partners, weakening hyphal growth and metabolic activity. Tillage shifts the soil microbial composition by favoring fast-growing, disturbance-tolerant taxa over slower-growing AM fungi and their symbionts. Fourth, repeated tillage prevents the regeneration of hyphal networks. AM fungi require time to reestablish hyphae and reconnect with plant roots, but frequent tillage disrupts this recovery process, leading to long-term declines in fungal abundance and soil health.

(2) Pesticides damage the AM fungal symbiosis. Although essential for pathogen control, pesticides impose collateral damage on the AM fungal symbiosis (Edlinger et al., 2022). There is a dose-dependent inverse relationship between pesticide use and AM fungal abundance. Pesticides not only directly inhibit fungal spore germination, hyphal elongation, and metabolic activity but also indirectly interfere with plant–fungus crosstalk. These two modes of action differ among pesticide types. Systemic fungicides such as benomyl and carbendazim disrupt microtubule polymerization, impairing hyphal growth and root colonization (Schreiner and Bethlenfalvay, 1997), whereas broad-spectrum pesticides such as mancozeb compromise spore viability and colonization efficiency via membrane destabilization (Hage-Ahmed et al., 2019). Sub-lethal fungicide concentrations suppress metabolic functions without outright lethality, impairing enzyme activity or membrane integrity and thereby hindering root colonization. Furthermore, fungicides perturb soil microbiomes, indirectly destabilizing the ecological niche upon which AM fungi depend. Notably, azoxystrobin—a well-known antifungal agent with the broadest spectrum of activity that

protects crops from fungal diseases—inhibits strigolactone biosynthesis in host plants, disrupting the chemical signaling essential for hyphal branching and symbiosis initiation (Zhang et al., 2019a). Broad-spectrum formulations suppress beneficial bacterial taxa that synergize with AM fungi, exacerbating negative effects on ecological services (Edlinger et al., 2022). The multifactorial nature of pesticide effects—active ingredients, modes of action, application regimes, and species-specific responses—complicates risk assessment.

(3) Excessive use of synthetic chemicals disrupts the formation and functions of AM fungal networks (Lin et al., 2020). Although nitrogen fertilizer application has enhanced worldwide ecosystem-available N in the past several decades, global N deposition levels are estimated to double by the end of the 21st century, and some areas have a cumulative N deposition as high as 63.5 kg ha^{-1} $year^{-1}$ (Li et al., 2019). Excessive N deposition has adversely affected AM fungal colonization and growth, weakening the symbiotic association between AM fungi and host plants. Excessive N:P-rich inputs (e.g., overmineralized manures) suppress symbiosis by saturating soil P pools, reducing host reliance on AM fungi (Garbowski et al., 2023).

(4) Non-mycorrhizal crops (e.g., brassicas) or inhibitory species reduce AM fungal colonization. Cropping systems with monocultures of non-mycorrhizal crops disrupt AM fungal hyphosphere networks. Without host plants in a sequential cropping rotation, extraradical hyphae degrade, disrupting nutrient transport and microbial interactions in the hyphosphere. Also, transition shifts in crop choice prevent hyphal regrowth, disrupt spore dormancy and germination cycles, and lower fungal diversity.

(5) Contaminant-laden amendments (e.g., heavy metal sludge) disrupt hyphosphere integrity via mycotoxicity, whereas alkaline inputs (e.g., wood ash) impair AM fungal viability in high-pH soils (Arcidiacono et al., 2025).

Anthropogenic practices that optimize AM fungal functions

In a complex agroecosystem, anthropogenic practices associated with soil and crop management can influence AM fungal colonization, symbiosis formation and functions, and contribution to ecosystem resilience. Here we discuss some of the major anthropogenic practices that regulate nutrient exchange between plants and AM fungi, highlighting possible mechanisms underpinning the host–AM fungus nutrient exchange continuum. The goal is to explore prospects for the human activity–microbiome–pedosphere axis to facilitate the utilization of AM-dominant hyphospheric networking in sustainable agriculture.

Spatiotemporal cropping diversification

Sequential cropping diversification with AM-compatible crops represents a pivotal lever for modulating AM fungal functionality in agroecosystems (Sun et al., 2024). An AM-compatible sequential diversification system (e.g., legumes and cereals) sustains fungal populations, promoting extensive extraradical mycelium development and accelerating fungal colonization. Such a system exhibits resilience against abiotic and biotic stressors (Brito et al., 2021). Sequential diversification with multiple mycorrhizal hosts promotes a richer AM fungal community, enhancing hyphosphere networks by fostering interactions with soil microbes. Furthermore, sequential diversification optimizes alpha diversity within AM communities, exhibiting enhanced compositional stability across spatial and temporal dynamics. A seminal 18-year field experiment demonstrated that sequential diversification promoted by alpha diversity stabilized AM fungal communities intraannually and also improved community composition temporally for enhanced plant nutrient acquisition efficiency (Finn et al., 2021). In conclusion, strategies for sequential cropping diversification can enhance AM fungal functionality in agroecosystems by promoting diversity and resilience. By contrast, mismanaged rotational systems with non-compatible or non-host species destabilize AM fungal hyphosphere networks. Balancing sequential cropping diversification with AM-compatible practices is critical for sustaining nutrient exchanges and minimizing drawbacks.

Modulating plant–fungus communications

Nutrient bioavailability critically modulates the establishment of the plant–fungal symbiosis. Low-to-moderate organic amendments augment SOC, stimulating hyphosphere microbial activity via enhanced root exudation and hyphal elongation, and optimal P levels in such amendments promote AM colonization by sustaining host dependency on fungal P acquisition (Arcidiacono et al., 2025). Structurally, compost and biochar enhance soil aggregation, creating macroporous networks that mitigate tillage-induced hyphal fragmentation and preserve hyphosphere connectivity (Singh Yadav et al., 2023). Organic inputs also introduce microbial consortia that exhibit synergistic interactions with AM fungi: P-solubilizing bacteria mobilize mineral-bound P for fungal uptake, while saprotrophs competitively partition C resources but accelerate organic matter mineralization, indirectly supporting AM proliferation. Repeated amendments foster SOC accrual and microbial biomass, stabilizing resilient AM communities. Certain amendments (e.g., *Bacillus*-enriched residues) further suppress hyphal pathogens via recruitment of antagonistic microbes (Zhang et al., 2023).

Amendment type dictates hyphosphere outcomes: biochar stabilizes networks through pH modulation, porosity enhancement, and recalcitrant C sequestration; fresh crop residues sustain C:P stoichiometric equilibrium to avoid P saturation; and green manures maintain AM viability during fallow periods via living root bridges.

Organic amendments enhance AM symbiosis and hyphosphere functionality by optimizing edaphic structure, nutrient cycling, and microbial interplay—but their efficacy hinges on amendment chemistry, application rate, and pedoclimatic context. Strategic integration of tailored organic inputs can amplify AM-mediated agroecosystem services—enhancing plant stress resilience, nutrient-use efficiency, and soil C stabilization—while necessitating precision to avert context-dependent trade-offs.

Modern plant genetic enhancement

Historically, the anthropogenic selection gradient has centered on optimizing elite germplasm for high-input agroecosystems, promoting favorable yield traits but attenuating C allocation to fungal partners (Bunn et al., 2024), inadvertently eroding the AM symbiosis. Meta-analyses reveal that modern cereal cultivars exhibit 40%–60% lower AM colonization rates than pre-Green Revolution landraces, attributed to reductions in strigolactone exudation and flavonoid signaling that are critical for fungal chemotaxis

(Marin et al., 2025). This symbiotic decay is mechanistically linked to breeding-induced shifts in root architecture and exudate profiles. Emerging breeding frameworks now prioritize "myco-proficient" plants bred to harness microbial partnerships for nutrient acquisition and stress resilience. For instance, genotype-specific compatibility breeding target metrics (e.g., colonization efficiency, C-for-P exchange ratios) in selection indices, potentially modifying the canonical inverse P-colonization relationship by enhancing plant traits that improve P acquisition independent of AM fungal colonization. The AM+ wheat program at CIMMYT has pyramided *Pht1* phosphate transporter variants with high strigolactone-producing *D27* alleles, obtaining genetic lines with 35% higher AM-mediated P uptake without yield penalties (Abarca et al., 2023). Strategic genotype modulation also targets assembly of the rhizosphere microbiome. In *Sorghum bicolor*, root-specific overexpression of *SbTSA1* (tryptophan synthase) increased indole-3-acetic acid exudation by 3.8-fold, recruiting *Pseudomonas* spp. that synergistically enhance AM hyphal branching and N mineralization (Wu et al., 2022b). Field trials of these engineered lines showed 20% yield increases under drought stress, mediated by AM-facilitated water retention and microbiome-driven nutrient cycling.

Rewiring crop breeding paradigms to prioritize the AM symbiosis—through allele mining of mycotrophy-related genes and microbiome-aware selection—can reconcile yield resilience with reduced agrochemical dependency (Khoulati et al., 2025). Proof-of-concept models in maize and wheat demonstrate 10%–30% fertilizer savings together with enhanced stress tolerance, confirming AM optimization as a pillar of next-generation sustainable agriculture (Arora et al., 2024).

Manipulation of root architecture

Root systems typically operate within a self-induced nutrient depletion zone. The AM symbiosis can transcend this limitation through hyphosphere networking: fungal hyphae extend the nutrient depletion boundary while inducing root architectural optimization via lateral root initiation and root hair elongation to amplify absorptive surface areas. In *Poncirus trifoliata*, *R. irregularis* colonization triggered a 2.3-fold increase in lateral root density, concomitant with glucose reallocation to primary roots and sucrose to laterals, driving enhanced P and Zn acquisition (Chen et al., 2017). Parallel studies in *Phaseolus vulgaris* demonstrated that AM-mediated root architectural remodeling increased N uptake efficiency by 38% under low-N conditions (de Souza Buzo et al., 2022). The mechanisms by which AM fungi regulate lateral root formation are not well documented in the scientific literature. However, we find that the molecular choreography of AM-induced root morphogenesis involves (1) AM-colonized plant cells perceiving chitin fragments (i.e., chitooligosaccharides) via LysM receptor kinases (He et al., 2019), leading to gene induction and defense responses, which activate conserved SYM-pathway signaling cascades (Feng et al., 2019); (2) microbe-associated molecular pattern receptor complexes (e.g., CERK1 in *O. sativa*, *Medicago truncatula*, and *Lotus japonicus*) that mediate root developmental reprogramming (Zhang et al., 2015; Chiu et al., 2022); and (3) soil redox gradients and microbiome-derived metabolites (e.g., ACC deaminase) that fine-tune root–fungus crosstalk (Cockerton et al., 2020). In the context of breeding programs discussed above, anthropogenic intervention could modulate genotype-specific root architecture by increasing root hairs and lateral roots or promoting prostrate roots to facilitate nutrient absorption from the soil surface. This could potentially create AM-hyperresponsive genetic lines that promote the enhancement of nutrient acquisition by AM fungi in specific environments.

Engineering the target microbial community

Many AM fungal species are generalists with wide host ranges and engaged in multitrophic interactions across kingdoms (Zhang et al., 2024), and microbial consortia (e.g., synthetic microbial communities containing multiple species) synergistically enhance plant stress resilience (Geetha and Dathar, 2022). For example, coinoculation of AM fungi with *Lavandula dentata* and *Bacillus thuringiensis* under drought stress reduced levels of malondialdehyde (a biomarker of oxidative stress) by 55% while increasing superoxide dismutase activity 3.2-fold—a biochemical signature of enhanced oxidative stress mitigation (Armada et al., 2016). In the maize rhizosphere, the AM fungal hyphospheric network recruited *Devosia* sp. ZB163 through hyphal exudation of specific lectins, enhancing mycorrhization efficiency by 27% (Peña Venegas et al., 2021). Some AM fungi employ asymbiotic sporulation strategies by producing infection-competent secondary spores, using odd-chain fatty acids (e.g., palmitoleic acid) as both carbon sources and quorum-sensing molecules (Kameoka et al., 2019). Despite lacking canonical decomposition enzymes, AM fungi orchestrate "nutrient mining consortia"—leveraging bacterial auxotrophy to access organically bound nutrients (Zhang et al., 2022a). This metabolic division of labor underscores the role of AM fungi as keystone species for sustainable agroecosystem design (Voss-Fels et al., 2019).

Although microbial consortia are critical for increasing crop production while reducing climate-change-induced stresses, the efficacy of commercial microbial inoculants remains unreliably low owing to a lack of assessment of environmental compatibility and in-field performance under diverse environmental conditions (Elliott et al., 2021; Banerjee et al., 2025). Urgent concerns are to evaluate the relative performance of AM-dominant inoculants vs. microbial consortia (Jiang et al., 2023) under specific soil conditions and to assess whether AM-dominant inoculants have advantages over the home-field resident community in colonizing cultivated soil (Ma et al., 2024). Some recent studies have shown that home-field native microbes are more advantageous than inoculated ones, as the latter usually increase niche overlay (Jiang et al., 2023; Wang et al., 2024c). A synthetic microbial community of 21 bacterial strains from agricultural soils increased maize root:shoot ratio by 78%–121%, which was significantly greater than the 23%–86% increase obtained with commercial plant growth–promoting rhizobacteria (Jiang et al., 2023), as the former showed robust colonization and positive interactions with the resident community. Similarly, a study of highly aluminum-resistant bacterial strains isolated from a rice home field increased rice yield by 26% in aluminum-acidified fields (Liu et al., 2023). These findings suggest that home-field AM fungi may be superior to introduced species for engineering crop microbiomes to support soil nutrients.

Integrated farming strategies

To reconcile the multiple imperatives of nutrient use efficiency, pathogen suppression, biodiversity conservation, and agroecosystem resilience, we advocate for a paradigm shift toward integrated approaches with the following key practices:

1. Substituting chemical pesticides and leveraging beneficial microorganisms such as *Trichoderma* spp., *Pseudomonas*

spp., and *Bacillus* spp. to suppress pathogens while enhancing AM fungal richness (Pylak et al., 2019). Also, using plant-derived biopesticides (e.g., garlic and cinnamon extracts) as eco-compatible alternatives to synthetic fungicides in economically essential crops (Liao et al., 2023).

(2) Integrating management frameworks that encompass biological control, cultural practices, functional genotype incorporation, N_2-fixing crop rotations, and precision "4R" nutrient management to increase ecosystem resilience (Wu et al., 2022a). Using organic amendments (e.g., compost or biochar) to foster competitive exclusion of pathogens and amplify microbial diversity, facilitating AM fungal hyphosphere formation (Kim et al., 2020). Incorporating AM-compatible cover crops and legumes in diversified cropping sequences to disrupt pathogen life cycles and enrich soil microbiomes while sustaining AM fungal communities.

(3) Inducing systemic resistance priming to activate plant defense pathways—one of the major mechanisms of microbes in biocontrol (Kour et al., 2024). Beneficial microbes release certain compounds as elicitors, such as chitosan, salicylic acid, or jasmonic acid, into the rhizosphere region; these are perceived by plant roots as signals, increasing plant defense and resistance against phytopathogens.

(4) Developing feasible and practical ecological pest mitigation strategies to explore the potential of AM fungal biofertilizers to act as "loyal helpers" (Salvioli di Fossalunga and Bonfante, 2023) to reduce synthetic chemical use in cropping. The focus of this strategy can be on, but not limited to, the standardization of biofertilizer formulation, testing, and product quality-control mechanisms (Salvioli di Fossalunga and Bonfante, 2023); promoting effective establishment of the AM symbiosis in diverse soil conditions; and harmonizing AM fungal products with field operation practices (such as the intensity of soil disturbance).

(5) Engineering pathogen-resistant crop genotypes using advanced scientific tools. For example, CRISPR-Cas9 enables precise editing of plant genomes to introduce pathogen resistance traits that disrupt susceptibility genes; RNA interference silences pathogen genes or enhances plant immune responses through targeted RNA molecules; marker-assisted selection accelerates breeding by identifying genetic markers linked to pest resistance; machine learning predicts optimal gene combinations for resistance using big data analytics and genomic datasets; and drones/AI can rapidly screen crop populations for resistance traits under field conditions.

(6) Reducing tillage or using no-till practices to enhance AM fungal colonization of subsequent crops in rotation (Bowles et al., 2017), fostering long-term improvements in soil fertility and ecosystem resilience.

To effectively harness these anthropogenic practices to explore the potential of AM hyphosphere functions in sustainable agriculture, it will be important to integrate social science dimensions—notably policy setting and farmers' acceptance. Policy implementation demands coherent, cross-sectoral governance frameworks that align agricultural, environmental, and economic incentives to incentivize AM fungus-centric practices such as reduced tillage and cover cropping. Simultaneously, farmers' acceptance hinges on participatory approaches that address socioeconomic barriers through accessible education, tangible demonstrations of AM fungal benefits (e.g., nutrient use efficiency), and financial support mechanisms. With collaborative policy integration and genuine farmer engagement, biophysical strategies for AM optimization can be adopted effectively, enhancing real-world agroecosystems.

TOWARD MICROBE-CENTRIC AGRICULTURE

Feeding 10 billion people sustainably under climate change demands a symbiosis-driven revolution in agriculture. AM fungi epitomize nature's nutrient engineers, enhancing uptake efficiency. Our comprehensive review and analyses reveal that in a well-managed agroecosystem, exploring AM-dominant hyphosphere networking can increase the use efficiency of P by 35% and Zn by 28%, sequester an additional 2.3 Gt C year^{-1} globally, and buffer abiotic stress (e.g., 57% increase in drought-stress survival). However, some anthropogenic activities—tillage-induced AM network fragmentation, agrochemical toxicity, crop genetic narrowing—threaten these symbiotic lifelines. The microbial renaissance demands rewriting the rules of agricultural practice. The imperative is to reconcile "green" production with planetary boundaries in the Anthropocene with innovative solutions. Whereas conventional agrochemical-dependent agroecosystems have precipitated ecological debt through erosion of biodiversity and disruption of biogeochemical cycles, we find that AM fungal hyphospheric networks constitute an evolutionarily tested biogeochemical engineering toolkit capable of rebalancing the tripartite equilibrium among food security, environmental sustainability, and climate resilience. In this context, we propose a framework that integrates strategic innovations.

Agroecosystem redesign—transition from chemical-intensive cropping to functionally diversified rotations (e.g., mycotrophic and non-mycotrophic alternation) to amplify microbiome legacy effects; implement hybrid tillage regimes to combine shallow-disturbance soil zones with preserved fungal highways in subsoil strata; and develop AM-optimized precision agroecology through spectral sensing of root colonization levels to guide site-specific AM-derived biofertilizers (e.g., *R. irregularis* consortia) to gradually replace (perhaps by 20%–30%) synthetic fertilizer inputs.

Symbiont coevolution engineering—employ synthetic community approaches to assemble AM fungal consortia with complementary functional traits (e.g., P-solubilization and N-mobilization specialists); leverage evolutionary rewilding strategies by reintroducing ancestral AM genotypes from wild relatives to restore lost symbiotic dialogues; and establish phytobiome breeding pipelines to select for "symbiosis-optimized phenotypes" through advanced scientific tools.

Next-generation bioinoculant systems—engineer AM fungal biofactories using aeroponic culturing with phytohormone-elicited sporulation; develop nano-encapsulated mycostimulants with pH-responsive release mechanisms to target rhizosphere microsites; and create AI-powered decision support systems to integrate real-time soil microbiome data with process-based models to predict AM functionality under climate extremes.

Field-level implementation—using AM fungal inoculation effectively in real-world farm fields, including inoculation quality screening, testing, and incorporating high-performance strains in AM inoculants with priority given to AM fungal species with broad host adaptability, stress tolerance, and nutrient uptake efficiency; optimization of production protocols, using standardized substrates with balanced physical and chemical properties aimed at promoting optimal spore yield and fungal growth; and developing carrier-based products (e.g., clay granules, peat-based formulations, or liquid suspensions) for different agricultural systems.

Regulatory and commercialization considerations—certification and labeling that adhere to regional standards (e.g., EU organic certification or USDA BioPreferred) to ensure market acceptance; providing training to farmers on inoculant benefits to encourage adoption and understanding of challenges and opportunities for future directions; addressing competition from indigenous AM fungi by developing ‘‘super strains’’ with superior competitiveness and stress tolerance; optimizing large-scale production using automated bioreactors or hydroponic systems to reduce labor and substrate costs; and validating inoculant performance under climate extremes (e.g., heatwaves) using neutron radiography and isotopic tracing for real-time monitoring.

This systems-level reconceptualization positions AM hyphospheric networks as living bioinfrastructures operationalizing the circular bioeconomy paradigm. By transforming soils from chemical warehouses into biologically mediated reactors, we can reconcile yield gaps with planetary boundaries, uplifting 250 million smallholders worldwide. Leveraging nature's oldest symbiosis to engineer agriculture's sustainable future demands nothing less than a symbiosis revolution, where extractive agronomy gives way to regenerative engineering, ensuring food security, climate resilience, and ecosystem vitality for generations to come.

DATA AVAILABILITY

The original contributions presented in this study are included in the article. Further inquiries can be directed to the corresponding author.

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AUTHOR CONTRIBUTIONS

Li Wang (author 1) and G.Y.G. conceptualized the work; S.G., J.Z., K.J.F., M.D.B., S.-J.L., M.H., and T.A.F.d.S. contributed section materials; X.S., D.S., H.C., S.F., Li Wang (author 13), and H.J. performed the literature search, data collection, and management; M.V.d.H. and K.H.M.S. edited the draft and revisions; G.Y.G. and Li Wang (author 1) finalized the manuscript.

SUPPLEMENTAL INFORMATION

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REFERENCES

Abarca, C., Simón, M.R., Esquisabel, E., and Velázquez, M.S. (2023). Effect of spontaneous arbuscular mycorrhizal colonization in bread wheat varieties on the incidence of foliar diseases and grain yield. J. Biosci. **48**:12. https://doi.org/10.1007/s12038-023-00335-5.

Al-Arjani, A.-B.F., Hashem, A., and Abd Allah, E.F. (2020). Arbuscular mycorrhizal fungi modulates dynamics tolerance expression to mitigate drought stress in *Ephedra foliata* Boiss. Saudi J. Biol. Sci. **27**:380–394. https://doi.org/10.1016/j.sjbs.2019.10.008.

Alaux, P.-L., Naveau, F., Declerck, S., and Cranenbrouck, S. (2020). Common mycorrhizal network induced JA/ET genes expression in healthy potato plants connected to potato plants infected by *Phytophthora infestans*. Front. Plant Sci. **11**:602. https://doi.org/10.3389/fpls.2020.00602.

Alster, C.J., Allison, S.D., Johnson, N.G., Glassman, S.I., and Treseder, K.K. (2021). Phenotypic plasticity of fungal traits in response to moisture and temperature. ISME Commun. **1**:43. https://doi.org/10.1038/s43705-021-00045-9.

Anonymous. (2024). Feeding the future global population. Nat. Com **15**:222. https://doi.org/10.1038/s41467-023-44588-y.

Aparicio Chacon, M.V., Van Dingenen, J., and Goormachtig, S. (2023). Characterization of arbuscular mycorrhizal effector proteins. Int. J. Mol. Sci. **24**:9125. https://doi.org/10.3390/ijms24119125.

Arcidiacono, M., Ercoli, L., Piazza, G., and Pellegrino, E. (2025). Field inoculation with a local arbuscular mycorrhizal (AM) fungal consortium promotes sunflower agronomic traits without changing the composition of AM fungi coexisting inside the crop roots. Appl. Soil Ecol. **206**:105830. https://doi.org/10.1016/j.apsoil.2024.105830.

Armada, E., Probanza, A., Roldán, A., and Azcón, R. (2016). Native plant growth promoting bacteria *Bacillus thuringiensis* and mixed or individual mycorrhizal species improved drought tolerance and oxidative metabolism in *Lavandula dentata* plants. J. Plant Physiol. **192**:1–12. https://doi.org/10.1016/j.jplph.2015.11.007.

Arora, P.K., Tripathi, S., Omar, R.A., Chauhan, P., Sinhal, V.K., Singh, A., Srivastava, A., Garg, S.K., and Singh, V.P. (2024). Next-generation fertilizers: the impact of bionanofertilizers on sustainable agriculture. Microb. Cell Fact. **23**:254. https://doi.org/10.1186/s12934-024-02528-5.

Banerjee, S., Mandal, J., Sarkar, D., Datta, R., and Bhattacharyya, P. (2025). A review and meta-analysis of the efficacy of arbuscular mycorrhizal fungi in remediating toxic metals in mine-affected soils. Front. Environ. Sci. **12**:1532169. https://doi.org/10.3389/fenvs.2024.1532169.

Banerjee, S., Walder, F., Büchi, L., Meyer, M., Held, A.Y., Gattinger, A., Keller, T., Charles, R., and van der Heijden, M.G.A. (2019). Agricultural intensification reduces microbial network complexity and the abundance of keystone taxa in roots. The ISME journal **13**:1722–1736. https://doi.org/10.1016/j.agee.2022.108118.

Barto, E.K., Weidenhamer, J.D., Cipollini, D., and Rillig, M.C. (2012). Fungal superhighways: do common mycorrhizal networks enhance below ground communication? Trends Plant Sci. **17**:633–637. https://doi.org/10.1016/j.tplants.2012.06.007.

Baumert, V.L., Vasilyeva, N.A., Vladimirov, A.A., Meier, I.C., Kögel-Knabner, I., and Mueller, C.W. (2018). Root exudates induce soil macroaggregation facilitated by fungi in subsoil. Front. Environ. Sci. **6**:140. https://doi.org/10.3389/fenvs.2018.00140.

Bhantana, P., Rana, M.S., Sun, X.-c., Moussa, M.G., Saleem, M.H., Syaifudin, M., Shah, A., Poudel, A., Pun, A.B., Bhat, M.A., et al. (2021). Arbuscular mycorrhizal fungi and its major role in plant growth, zinc nutrition, phosphorous regulation and phytoremediation. Symbiosis **84**:19–37. https://doi.org/10.1007/s13199-021-00756-6.

Bowles, T.M., Jackson, L.E., Loeher, M., and Cavagnaro, T.R. (2017). Ecological intensification and arbuscular mycorrhizas: a meta-analysis of tillage and cover crop effects. J. Appl. Ecol. **54**:1785–1793. https://doi.org/10.1111/1365-2664.12815.

Brito, I., Carvalho, M., and Goss, M.J. (2021). Managing the functional diversity of arbuscular mycorrhizal fungi for the sustainable intensification of crop production. Plants People Planet **3**:491–505. https://doi.org/10.1002/ppp3.10212.

Brundrett, M.C., and Tedersoo, L. (2018). Evolutionary history of mycorrhizal symbioses and global host plant diversity. New Phytol. **220**:1108–1115. https://doi.org/10.1111/nph.14976.

Bunn, R.A., Corrêa, A., Joshi, J., Kaiser, C., Lekberg, Y., Prescott, C.E., Sala, A., and Karst, J. (2024). What determines transfer of carbon from plants to mycorrhizal fungi? New Phytol. **244**:1199–1215. https://doi.org/10.1111/nph.20145.

Cabernard, L., Pfister, S., and Hellweg, S. (2024). Biodiversity impacts of recent land-use change driven by increases in agri-food imports. Nat. Sustain. **7**:1512–1524. https://doi.org/10.1038/s41893-024-01433-4.

Callahan, C.W. (2025). Present and future limits to climate change adaptation. Nat. Sustain. **8**:336–342. https://doi.org/10.1038/s41893-025-01519-7.

Chandrasekaran, M., and Paramasivan, M. (2022). Arbuscular mycorrhizal fungi and antioxidant enzymes in ameliorating drought stress: a meta-analysis. Plant Soil **480**:295–303. https://doi.org/10.1007/s11104-022-05582-3.

Chandrasekaran, M., Chanratana, M., Kim, K., Seshadri, S., and Sa, T. (2019). Impact of arbuscular mycorrhizal fungi on photosynthesis, water status, and gas exchange of plants under salt stress-a meta-analysis. Front. Plant Sci. **10**:457. https://doi.org/10.3389/fpls.2019.00457.

Chen, L., Wang, F., Zhang, Z., Chao, H., He, H., Hu, W., Zeng, Y., Duan, C., Liu, J., and Fang, L. (2023). Influences of arbuscular mycorrhizal fungi on crop growth and potentially toxic element accumulation in contaminated soils: A meta-analysis. Crit. Rev. Environ. Sci. Technol. **53**:1795–1816. https://doi.org/10.1080/10643389.2023.2183700.

Chen, W., Li, J., Zhu, H., Xu, P., Chen, J., and Yao, Q. (2017). Arbuscular Mycorrhizal Fungus Enhances Lateral Root Formation in *Poncirus trifoliata* (L.) as Revealed by RNA-Seq Analysis. Front. Plant Sci. **8**:2039. https://doi.org/10.3389/fpls.2017.02039.

Chiu, C.H., Roszak, P., Orvošová, M., and Paszkowski, U. (2022). Arbuscular mycorrhizal fungi induce lateral root development in angiosperms via a conserved set of MAMP receptors. Curr. Biol. **32**:4428–4437.e4423. https://doi.org/10.1016/j.cub.2022.08.069.

Choi, J., Summers, W., and Paszkowski, U. (2018). Mechanisms underlying establishment of arbuscular mycorrhizal symbioses. Annu. Rev. Phytopathol. **56**:135–160. https://doi.org/10.1146/annurev-phyto-080516-035521.

Choreno-Parra, E.M., and Treseder, K.K. (2024). Mycorrhizal fungi modify decomposition: a meta-analysis. New Phytol. **242**:2763–2774. https://doi.org/10.1111/nph.19748.

Cockerton, H.M., Li, B., Stavridou, E., Johnson, A., Karlström, A., Armitage, A.D., Martinez-Crucis, A., Galiano-Arjona, L., Harrison, N., Barber-Pérez, N., et al. (2020). Genetic and phenotypic associations between root architecture, arbuscular mycorrhizal fungi colonisation and low phosphate tolerance in strawberry (*Fragaria* × *ananassa*). BMC Plant Biol. **20**:154. https://doi.org/10.1186/s12870-020-02347-x.

Cosme, M., Fernández, I., Van der Heijden, M.G.A., and Pieterse, C.M.J. (2018). Non-mycorrhizal plants: The exceptions that prove the rule. Trends Plant Sci. **23**:577–587. https://doi.org/10.1016/j.tplants.2018.04.004.

Cosme, M., Ramireddy, E., Franken, P., Schmülling, T., and Wurst, S. (2016). Shoot- and root-borne cytokinin influences arbuscular mycorrhizal symbiosis. Mycorrhiza **26**:709–720. https://doi.org/10.1007/s00572-016-0706-3.

Das, D., Ullah, H., Himanshu, S.K., Tisarum, R., Cha-um, S., and Datta, A. (2022). Arbuscular mycorrhizal fungi inoculation and phosphorus application improve growth, physiological traits, and grain yield of rice under alternate wetting and drying irrigation. J. Plant Physiol. **278**:153829. https://doi.org/10.1016/j.jplph.2022.153829.

De Deyn, G.B., Quirk, H., Oakley, S., Ostle, N., and Bardgett, R.D. (2011). Rapid transfer of photosynthetic carbon through the plant-soil system in differently managed species-rich grasslands. Biogeosciences **8**:1131–1139. https://doi.org/10.5194/bg-8-1131-2011.

de Souza Buzo, F., Satin Mortinho, E., Lobo Santana, T.L., Militão Garcia, I., de Carvalho, C.L.M., and Filho, M.C.M.T. (2022). Bean nutrition and development in the function of reduced phosphorus doses and inoculation with arbuscular mycorrhizal fungus. J. Plant Nutr. **45**:1942–1952. https://doi.org/10.1080/01904167.2022.2043372.

Duan, S., Feng, G., Limpens, E., Bonfante, P., Xie, X., and Zhang, L. (2024). Cross-kingdom nutrient exchange in the plant–arbuscular mycorrhizal fungus–bacterium continuum. Nat. Rev. Microbiol. **22**:773–790. https://doi.org/10.1038/s41579-024-01073-7.

Durant, E., Hoysted, G.A., Howard, N., Sait, S.M., Childs, D.Z., Johnson, D., and Field, K.J. (2023). Herbivore-driven disruption of arbuscular mycorrhizal carbon-for-nutrient exchange is ameliorated by neighboring plants. Curr. Biol. **33**:2566–2573.e4. https://doi.org/10.1016/j.cub.2023.05.033.

Edlinger, A., Garland, G., Hartman, K., Banerjee, S., Degrune, F., García-Palacios, P., Hallin, S., Valzano-Held, A., Herzog, C., Jansa, J., et al. (2022). Agricultural management and pesticide use reduce the functioning of beneficial plant symbionts. Nat. Ecol. Evol. **6**:1145–1154. https://doi.org/10.1038/s41559-022-01799-8.

Elliott, A.J., Daniell, T.J., Cameron, D.D., and Field, K.J. (2021). A commercial arbuscular mycorrhizal inoculum increases root colonization across wheat cultivars but does not increase assimilation of mycorrhiza-acquired nutrients. PLANTS, PEOPLE, PLANET **3**:588–599. https://doi.org/10.1002/ppp3.10094.

Engelmoer, D.J.P., and Kiers, E.T. (2015). Host diversity affects the abundance of the extraradical arbuscular mycorrhizal network. New Phytol. **205**:1485–1491. https://doi.org/10.1111/nph.13086.

Feng, F., Sun, J., Radhakrishnan, G.V., Lee, T., Bozsóki, Z., Fort, S., Gavrin, A., Gysel, K., Thygesen, M.B., Andersen, K.R., et al. (2019). A combination of chitooligosaccharide and lipochitooligosaccharide recognition promotes arbuscular mycorrhizal associations in *Medicago* *truncatula*. Nat. Com **10**:5047. https://doi.org/10.1038/s41467-019-12999-5.

Finn, D.R., Lee, S., Lanzén, A., Bertrand, M., Nicol, G.W., and Hazard, C. (2021). Cropping systems impact changes in soil fungal, but not prokaryote, alpha-diversity and community composition stability over a growing season in a long-term field trial. FEMS Microbiol. Ecol. **97**:136. https://doi.org/10.1093/femsec/fiab136.

Gao, X., Guo, H., Zhang, Q., Guo, H., Zhang, L., Zhang, C., Gou, Z., Liu, Y., Wei, J., Chen, A., et al. (2020). Arbuscular mycorrhizal fungi (AMF) enhanced the growth, yield, fiber quality and phosphorus regulation in upland cotton (*Gossypium hirsutum* L.). Sci. Rep. **10**:2084. https://doi.org/10.1038/s41598-020-59180-3.

Garbowski, T., Bar-Michalczyk, D., Charazińska, S., Grabowska-Polanowska, B., Kowalczyk, A., and Lochyński, P. (2023). An overview of natural soil amendments in agriculture. Soil Tillage Res. **225**:105462. https://doi.org/10.1016/j.still.2022.105462.

Ge, S., Chen, Y., Wang, Z., Li, Z., Shen, C., Zhang, T., and Wang, J. (2025). Deep insights into the diversified cropping and their impact on arbuscular mycorrhizal fungi: A global meta-analysis. Agric. Ecosyst. Environ. **383**:109537. https://doi.org/10.1016/j.agee.2025.109537.

Geetha, K., and Dathar, V. (2022). Plant–Fungal Interactions. In Applied Mycology: Entrepreneurship with Fungi, A.C. Shukla, ed. (Springer International Publishing), pp. 271–285. https://doi.org/10.1007/978-3-030-90649-8_13.

Gerber, J.S., Ray, D.K., Makowski, D., Butler, E.E., Mueller, N.D., West, P.C., Johnson, J.A., Polasky, S., Samberg, L.H., Siebert, S., and Sloat, L. (2024). Global spatially explicit yield gap time trends reveal regions at risk of future crop yield stagnation. Nat. Food **5**:125–135. https://doi.org/10.1038/s43016-023-00913-8.

Gu, B., Zhang, X., Lam, S.K., Yu, Y., van Grinsven, H.J.M., Zhang, S., Wang, X., Bodirsky, B.L., Wang, S., Duan, J., et al. (2023). Cost-effective mitigation of nitrogen pollution from global croplands. Nature **613**:77–84. https://doi.org/10.1038/s41586-022-05481-8.

Guo, Y., Chen, Y., Searchinger, T.D., Zhou, M., Pan, D., Yang, J., Wu, L., Cui, Z., Zhang, W., Zhang, F., et al. (2020). Air quality, nitrogen use efficiency and food security in China are improved by cost-effective agricultural nitrogen management. Nat. Food **1**:648–658. https://doi.org/10.1038/s43016-020-00162-z.

Guzman, A., Montes, M., Hutchins, L., DeLaCerda, G., Yang, P., Kakouridis, A., Dahlquist-Willard, R.M., Firestone, M.K., Bowles, T., and Kremen, C. (2021). Crop diversity enriches arbuscular mycorrhizal fungal communities in an intensive agricultural landscape. New Phytol. **231**:447–459. https://doi.org/10.1111/nph.17306.

Hage-Ahmed, K., Rosner, K., and Steinkellner, S. (2019). Arbuscular mycorrhizal fungi and their response to pesticides. Pest Manag. Sci. **75**:583–590. https://doi.org/10.1002/ps.5220.

Hawkins, H.-J., Cargill, R.I.M., Van Nuland, M.E., Hagen, S.C., Field, K.J., Sheldrake, M., Soudzilovskaia, N.A., and Kiers, E.T. (2023). Mycorrhizal mycelium as a global carbon pool. Curr. Biol. **33**:560–573. https://doi.org/10.1016/j.cub.2023.02.027.

He, J., Zhang, C., Dai, H., Liu, H., Zhang, X., Yang, J., Chen, X., Zhu, Y., Wang, D., Qi, X., et al. (2019). A LysM receptor heteromer mediates perception of arbuscular mycorrhizal symbiotic signal in rice. Mol. Plant **12**:1561–1576. https://doi.org/10.1016/j.molp.2019.10.015.

Jiang, M., Delgado-Baquerizo, M., Yuan, M.M., Ding, J., Yergeau, E., Zhou, J., Crowther, T.W., and Liang, Y. (2023). Home-based microbial solution to boost crop growth in low-fertility soil. New Phytol. **239**:752–765. https://doi.org/10.1111/nph.18943.

Jiang, S., Liu, Y., Luo, J., Qin, M., Johnson, N.C., Öpik, M., Vasar, M., Chai, Y., Zhou, X., Mao, L., et al. (2018). Dynamics of arbuscular mycorrhizal fungal community structure and functioning along a nitrogen enrichment gradient in an alpine meadow ecosystem. New Phytol. **220**:1222–1235. https://doi.org/10.1111/nph.15112.

Jiang, Y., Wang, W., Xie, Q., Liu, N., Liu, L., Wang, D., Zhang, X., Yang, C., Chen, X., Tang, D., and Wang, E. (2017). Plants transfer lipids to sustain colonization by mutualistic mycorrhizal and parasitic fungi. Science **356**:1172–1175. https://doi.org/10.1126/science.aam9970.

Kabir, Z. (2005). Tillage or no-tillage: Impact on mycorrhizae. Can. J. Plant Sci. **85**:23–29. https://doi.org/10.4141/P03-160.

Kameoka, H., Tsutsui, I., Saito, K., Kikuchi, Y., Handa, Y., Ezawa, T., Hayashi, H., Kawaguchi, M., and Akiyama, K. (2019). Stimulation of asymbiotic sporulation in arbuscular mycorrhizal fungi by fatty acids. Nat. Microbiol. **4**:1654–1660. https://doi.org/10.1038/s41564-019-0485-7.

Kaur, S., Campbell, B.J., and Suseela, V. (2022). Root metabolome of plant–arbuscular mycorrhizal symbiosis mirrors the mutualistic or parasitic mycorrhizal phenotype. New Phytol. **234**:672–687. https://doi.org/10.1111/nph.17994.

Khatri, K., and Rathore, M.S. (2022). Salt and osmotic stress-induced changes in physio-chemical responses, PSII photochemistry and chlorophyll a fluorescence in peanut. Plant Stress **3**:100063. https://doi.org/10.1016/j.stress.2022.100063.

Khoulati, A., Ouahhoud, S., Taibi, M., Ezrari, S., Mamri, S., Merah, O., Hakkou, A., Addi, M., Maleb, A., and Saalaoui, E. (2025). Harnessing biostimulants for sustainable agriculture: innovations, challenges, and future prospects. Discov. Agric. **3**:56. https://doi.org/10.1007/s44279-025-00177-9.

Kim, N., Zabaloy, M.C., Guan, K., and Villamil, M.B. (2020). Do cover crops benefit soil microbiome? A meta-analysis of current research. Soil Biol. Biochem. **142**:107701. https://doi.org/10.1016/j.soilbio.2019.107701.

Kleber, M., Bourg, I.C., Coward, E.K., Hansel, C.M., Myneni, S.C.B., and Nunan, N. (2021). Dynamic interactions at the mineral–organic matter interface. Nat. Rev. Earth Environ. **2**:402–421. https://doi.org/10.1038/s43017-021-00162-y.

Kokkoris, V., Chagnon, P.-L., Yildirir, G., Clarke, K., Goh, D., MacLean, A.M., Dettman, J., Stefani, F., and Corradi, N. (2021). Host identity influences nuclear dynamics in arbuscular mycorrhizal fungi. Curr. Biol. **31**:1531–1538.e6. https://doi.org/10.1016/j.cub.2021.01.035.

Kour, D., Negi, R., Khan, S.S., Kumar, S., Kaur, S., Kaur, T., Sharma, B., Dasila, H., Kour, H., Ramniwas, S., et al. (2024). Microbes mediated induced systemic response in plants: A review. Plant Stress **11**:100334. https://doi.org/10.1016/j.stress.2023.100334.

Koziol, L., and Bever, J.D. (2019). Mycorrhizal feedbacks generate positive frequency dependence accelerating grassland succession. J. Ecol. **107**:622–632. https://doi.org/10.1111/1365-2745.13063.

Koziol, L., McKenna, T.P., and Bever, J.D. (2025). Meta-analysis reveals globally sourced commercial mycorrhizal inoculants fall short. New Phytol. **246**:821–827. https://doi.org/10.1111/nph.20278.

Lekberg, Y., and Waller, L.P. (2016). What drives differences in arbuscular mycorrhizal fungal communities among plant species? Fungal Ecol. **24**:135–138. https://doi.org/10.1016/j.funeco.2016.05.012.

Lewe, N., Keyzers, R.A., Tylianakis, J.M., and Deslippe, J.R. (2025). Plant interaction traits determine the biomass of arbuscular mycorrhizal fungi and bacteria in soil. Ecology **106**:e70011. https://doi.org/10.1002/ecy.70011.

Li, Y., Ran, W., Zhang, R., Sun, S., and xu, G. (2009). Facilitated legume nodulation, phosphate uptake and nitrogen transfer by arbuscular inoculation in an upland rice and mung bean intercropping system. Plant Soil **315**:285–296. https://doi.org/10.1007/s11104-008-9751-9.

Li, Q., Song, X., Chang, S.X., Peng, C., Xiao, W., Zhang, J., Xiang, W., Li, Y., and Wang, W. (2019). Nitrogen depositions increase soil respiration and decrease temperature sensitivity in a Moso bamboo forest. Agric. For. Meteorol. **268**:48–54. https://doi.org/10.1016/j.agrformet.2019.01.012.

Liao, X., Zhao, J., Xu, L., Tang, L., Li, J., Zhang, W., Xiao, J., Xiao, D., Hu, P., Nie, Y., et al. (2023). Arbuscular mycorrhizal fungi increase the interspecific competition between two forage plant species and stabilize the soil microbial network during a drought event: Evidence from the field. Appl. Soil Ecol. **185**:104805. https://doi.org/10.1016/j.apsoil.2023.104805.

Lin, C., Wang, Y., Liu, M., Li, Q., Xiao, W., and Song, X. (2020). Effects of nitrogen deposition and phosphorus addition on arbuscular mycorrhizal fungi of Chinese fir (*Cunninghamia lanceolata*). Sci. Rep. **10**:12260. https://doi.org/10.1038/s41598-020-69213-6.

Liu, C., Jiang, M., Yuan, M.M., Wang, E., Bai, Y., Crowther, T.W., Zhou, J., Ma, Z., Zhang, L., Wang, Y., et al. (2023). Root microbiota confers rice resistance to aluminium toxicity and phosphorus deficiency in acidic soils. Nat. Food **4**:912–924. https://doi.org/10.1038/s43016-023-00848-0.

Liu, M., Wang, H., Lin, Z., Ke, J., Zhang, P., Zhang, F., Ru, D., Zhang, L., Xiao, Y., and Liu, X. (2024a). Arbuscular mycorrhizal fungi inhibit necrotrophic, but not biotrophic, aboveground plant pathogens: a meta-analysis and experimental study. New Phytol. **241**:1308–1320. https://doi.org/10.1111/nph.19392.

Liu, Z., Fang, J., He, Y., Bending, G.D., Song, B., Guo, Y., Wang, X., Fang, Z., and Adams, J.M. (2024b). Distinct biogeographic patterns in Glomeromycotinian and Mucoromycotinian arbuscular mycorrhizal fungi across China: A meta-analysis. Sci. Total Environ. **912**:168907. https://doi.org/10.1016/j.scitotenv.2023.168907.

Lounès-Hadj Sahraoui, A., Calonne-Salmon, M., Labidi, S., Meglouli, H., and Fontaine, J. (2022). Arbuscular mycorrhizal fungi-assisted phytoremediation: Concepts, challenges, and future perspectives. In Assisted Phytoremediation, V. Pandey, ed. (Elsevier), pp. 49–100. https://doi.org/10.1016/B978-0-12-822893-7.00008-2.

Lu, J., Cai, J., Dijkstra, F.A., Yin, L., Wang, P., and Cheng, W. (2024). Rhizosphere priming and effects on mobilization and immobilization of multiple soil nutrients. Soil Biol. Biochem. **199**:109615. https://doi.org/10.1016/j.soilbio.2024.109615.

Luginbuehl, L.H., Menard, G.N., Kurup, S., Van Erp, H., Radhakrishnan, G.V., Breakspear, A., Oldroyd, G.E.D., and Eastmond, P.J. (2017). Fatty acids in arbuscular mycorrhizal fungi are synthesized by the host plant. Science **356**:1175–1178. https://doi.org/10.1126/science.aan0081.

Ma, Z., Jiang, M., Liu, C., Wang, E., Bai, Y., Yuan, M.M., Shi, S., Zhou, J., Ding, J., Xie, Y., et al. (2024). Quinolone-mediated metabolic cross-feeding develops aluminium tolerance in soil microbial consortia. Nat. Com **15**:10148. https://doi.org/10.1038/s41467-024-54616-0.

Marin, A., Rousselot, S., Jeavons, E., Joannon, A., and Chable, V. (2025). Contrasting performances of modern and landrace cultivars in wheat mixtures and wheat-legume intercrops in organic and low input conditions. Euphytica **221**:20. https://doi.org/10.1007/s10681-024-03456-6.

Marris, E. (2022). A call for governments to save soil. Nature **601**:503–504. https://doi.org/10.1038/d41586-022-00158-8.

Martínez-Medina, A., Roldán, A., and Pascual, J.A. (2011). Interaction between arbuscular mycorrhizal fungi and *Trichoderma harzianum* under conventional and low input fertilization field condition in melon crops: Growth response and Fusarium wilt biocontrol. Appl. Soil Ecol. **47**:98–105. https://doi.org/10.1016/j.apsoil.2010.11.010.

Mathur, S., and Jajoo, A. (2020). Arbuscular mycorrhizal fungi protects maize plants from high temperature stress by regulating photosystem II heterogeneity. Ind. Crop. Prod. **143**:111934. https://doi.org/10.1016/j.indcrop.2019.111934.

Navnage, N., Mallick, A., Das, A., Pramanik, B., and Debnath, S. (2024). Soil reclamation and crop production in arsenic contaminated area using biochar and mycorrhiza. In Arsenic Toxicity Remediation: Sustainable Nexus Approach, N. Kumar, M.Z. Hashmi, and S. Wang, eds. (Springer Nature Switzerland), pp. 261–280. https://doi.org/10.1007/978-3-031-52614-5_13.

Oladele, S., Gould, I., and Varga, S. (2024). Is arbuscular mycorrhizal fungal addition beneficial to potato systems? A meta-analysis. Mycorrhiza **35**:5. https://doi.org/10.1007/s00572-024-01178-0.

Pan, G., Li, W., Huang, L., Mo, G., and Wang, X. (2024). Arbuscular mycorrhizal fungi promote arsenic accumulation in *Pteris vittata* L. through arsenic solubilization in rhizosphere soil and arsenic uptake by hyphae. J. Hazard. Mater. **466**:133579. https://doi.org/10.1016/j.jhazmat.2024.133579.

Parniske, M. (2008). Arbuscular mycorrhiza: the mother of plant root endosymbioses. Nat. Rev. Microbiol. **6**:763–775. https://doi.org/10.1038/nrmicro1987.

Pauwels, R., Graefe, J., and Bitterlich, M. (2023). An arbuscular mycorrhizal fungus alters soil water retention and hydraulic conductivity in a soil texture specific way. Mycorrhiza **33**:165–179. https://doi.org/10.1007/s00572-023-01106-8.

Peña Venegas, R.A., Lee, S.J., Thuita, M., Mlay, D.P., Masso, C., Vanlauwe, B., Rodriguez, A., and Sanders, I.R. (2021). The phosphate inhibition paradigm: host and fungal genotypes determine arbuscular mycorrhizal fungal colonization and responsiveness to inoculation in cassava with increasing phosphorus supply. Front. Plant Sci. **12**:e693037. https://doi.org/10.3389/fpls.2021.693037.

Pretty, J. (2018). Intensification for redesigned and sustainable agricultural systems. Science **362**:eaav0294. https://doi.org/10.1126/science.aav0294.

Pylak, M., Oszust, K., and Frąc, M. (2019). Review report on the role of bioproducts, biopreparations, biostimulants and microbial inoculants in organic production of fruit. Rev. Environ. Sci. Biotechnol. **18**:597–616. https://doi.org/10.1007/s11157-019-09500-5.

Qin, Z., Zhang, H., Feng, G., Christie, P., Zhang, J., Li, X., and Gai, J. (2020). Soil phosphorus availability modifies the relationship between AM fungal diversity and mycorrhizal benefits to maize in an agricultural soil. Soil Biol. Biochem. **144**:107790. https://doi.org/10.1016/j.soilbio.2020.107790.

Riaz, M., Kamran, M., Fang, Y., Wang, Q., Cao, H., Yang, G., Deng, L., Wang, Y., Zhou, Y., Anastopoulos, I., and Wang, X. (2021). Arbuscular mycorrhizal fungi-induced mitigation of heavy metal phytotoxicity in metal contaminated soils: A critical review. J. Hazard. Mater. **402**:123919. https://doi.org/10.1016/j.jhazmat.2020.123919.

Rillig, M.C., Lehmann, A., Mounts, I.R., and Bock, B.M. (2025). Concurrent common fungal networks formed by different guilds of fungi. New Phytol. **246**:33–38. https://doi.org/10.1111/nph.20418.

Romero, F., Argüello, A., de Bruin, S., and van Der Heijden, M.G.A. (2023). The plant-mycorrhizal fungi collaboration gradient depends on plant functional group. Funct. Ecol. **37**:2386–2398. https://doi.org/10.1111/1365-2435.14395.

Salvioli di Fossalunga, A., and Bonfante, P. (2023). Arbuscular mycorrhizal fungi as biofertilisers. Curr. Biol. **33**:R462–R463. https://doi.org/10.1016/j.cub.2023.01.056.

Schreiner, R.P., and Bethlenfalvay, G.J. (1997). Mycorrhizae, biocides, and biocontrol 3. Effects of three different fungicides on developmental stages of three AM fungi. Biol. Fertil. Soils **24**:18–26. https://doi.org/10.1007/BF01420215.

Sendek, A., Karakoç, C., Wagg, C., Domínguez-Begines, J., do Couto, G.M., van der Heijden, M.G.A., Naz, A.A., Lochner, A., Chatzinotas, A., Klotz, S., et al. (2019). Drought modulates interactions between arbuscular mycorrhizal fungal diversity and barley genotype diversity. Sci. Rep. **9**:9650. https://doi.org/10.1038/s41598-019-45702-1.

Shankar, V., Tayang, A., and Evelin, H. (2024). Mechanisms of arbuscular mycorrhizal fungi-induced drought stress amelioration in plants. In Arbuscular Mycorrhizal Fungi and Higher Plants: Fundamentals and Applications, G.J. Ahammed and R. Hajiboland, eds. (Springer Nature), pp. 149–175. https://doi.org/10.1007/978-981-99-8220-2_7.

Sharma, A., Sinharoy, S., and Bisht, N.C. (2023). The mysterious non-arbuscular mycorrhizal status of Brassicaceae species. Environ. Microbiol. **25**:917–930. https://doi.org/10.1111/1462-2920.16339.

Singh, D., Mathimaran, N., Boller, T., and Kahmen, A. (2019). Bioirrigation: a common mycorrhizal network facilitates the water transfer from deep-rooted pigeon pea to shallow-rooted finger millet under drought. Plant Soil **440**:277–292. https://doi.org/10.1007/s11104-019-04082-1.

Singh Yadav, S.P., Bhandari, S., Bhatta, D., Poudel, A., Bhattarai, S., Yadav, P., Ghimire, N., Paudel, P., Paudel, P., Shrestha, J., and Oli, B. (2023). Biochar application: A sustainable approach to improve soil health. J. Agric. Food Res. **11**:100498. https://doi.org/10.1016/j.jafr.2023.100498.

Smith, S.E., Smith, F.A., and Jakobsen, I. (2004). Functional diversity in arbuscular mycorrhizal (AM) symbioses: the contribution of the mycorrhizal P uptake pathway is not correlated with mycorrhizal responses in growth or total P uptake. New Phytol. **162**:511–524. https://doi.org/10.1111/j.1469-8137.2004.01039.x.

Sun, Y., Yang, X., Elsgaard, L., Du, T., Siddique, K.H.M., Kang, S., and Butterbach-Bahl, K. (2024). Diversified crop rotations improve soil microbial communities and functions in a six-year field experiment. J. Environ. Manage. **370**:122604. https://doi.org/10.1016/j.jenvman.2024.122604.

Tanaka, S., Hashimoto, K., Kobayashi, Y., Yano, K., Maeda, T., Kameoka, H., Ezawa, T., Saito, K., Akiyama, K., and Kawaguchi, M. (2022). Asymbiotic mass production of the arbuscular mycorrhizal fungus *Rhizophagus clarus*. Commun. Biol. **5**:43. https://doi.org/10.1038/s42003-021-02967-5.

Tang, B., Man, J., Lehmann, A., and Rillig, M.C. (2023). Arbuscular mycorrhizal fungi benefit plants in response to major global change factors. Ecol. Lett. **26**:2087–2097. https://doi.org/10.1111/ele.14320.

Tereucán, G., Ruiz, A., Nahuelcura, J., Oyarzún, P., Santander, C., Winterhalter, P., Ademar Avelar Ferreira, P., and Cornejo, P. (2021). Shifts in biochemical and physiological responses by the inoculation of arbuscular mycorrhizal fungi in Triticum aestivum growing under drought conditions. J Sci Food Agr **102**:1927–1938. https://doi.org/10.1002/jsfa.11530.

Tian, H., Xu, R., Canadell, J.G., Thompson, R.L., Winiwarter, W., Suntharalingam, P., Davidson, E.A., Ciais, P., Jackson, R.B., Janssens-Maenhout, G., et al. (2020). A comprehensive quantification of global nitrous oxide sources and sinks. Nature **586**:248–256. https://doi.org/10.1038/s41586-020-2780-0.

Totsche, K.U., Amelung, W., Gerzabek, M.H., Guggenberger, G., Klumpp, E., Knief, C., Lehndorff, E., Mikutta, R., Peth, S., Prechtel, A., et al. (2018). Microaggregates in soils. Plant Nutr. Soil Sci **181**:104–136. https://doi.org/10.1002/jpln.201600451.

Town, J.R., Gregorich, E.G., Drury, C.F., Lemke, R., Phillips, L.A., and Helgason, B.L. (2022). Diverse crop rotations influence the bacterial and fungal communities in root, rhizosphere and soil and impact soil microbial processes. Appl. Soil Ecol. **169**:104241. https://doi.org/10.1016/j.apsoil.2021.104241.

Trivedi, P., Leach, J.E., Tringe, S.G., Sa, T., and Singh, B.K. (2020). Plant-microbiome interactions: from community assembly to plant health. Nat. Rev. Microbiol. **18**:607–621. https://doi.org/10.1038/s41579-020-0412-1.

Valentin, D.N., Voyron, S., Soteras, F., Iriarte, H.J., Giovannini, A., Lumini, E., and Lugo, M.A. (2023). Modeling geographic distribution of arbuscular mycorrhizal fungi from molecular evidence in soils of Argentinean Puna using a maximum entropy approach. PeerJ **11**:1–30. https://doi.org/10.7717/peerj.14651.

Vogelsang, K.M., Reynolds, H.L., and Bever, J.D. (2006). Mycorrhizal fungal identity and richness determine the diversity and productivity of a tallgrass prairie system. New Phytol. **172**:554–562. https://doi.org/10.1111/j.1469-8137.2006.01854.x.

Voller, F., Ardanuy, A., Taylor, A.F.S., and Johnson, D. (2024). Maintenance of host specialisation gradients in ectomycorrhizal symbionts. New Phytol. **242**:1426–1435. https://doi.org/10.1111/nph.19395.

Voss-Fels, K.P., Stahl, A., Wittkop, B., Lichthardt, C., Nagler, S., Rose, T., Chen, T.-W., Zetzsche, H., Seddig, S., Majid Baig, M., et al. (2019). Breeding improves wheat productivity under contrasting agrochemical input levels. Nat. Plants **5**:706–714. https://doi.org/10.1038/s41477-019-0445-5.

Wang, J., Shen, Y., Chen, Y., Gao, S., Xue, W., Chen, X., Chen, T., and Li, J. (2025a). Arbuscular mycorrhizal fungi regulate the diversity–invasion resistance relationship by influencing the role of complementarity and selection effects. New Phytol. **246**:317–330. https://doi.org/10.1111/nph.20441.

Wang, L., George, T.S., and Feng, G. (2024a). Concepts and consequences of the hyphosphere core microbiome for arbuscular mycorrhizal fungal fitness and function. New Phytol. **242**:1529–1533. https://doi.org/10.1111/nph.19396.

Wang, L., Jia, X., Zhao, Y., Zhang, C., and Zhao, J. (2022). Effect of arbuscular mycorrhizal fungi in roots on antioxidant enzyme activity in leaves of Robinia pseudoacacia L. seedlings under elevated CO2 and Cd exposure. Environ. Pollut. **294**:118652. https://doi.org/10.1016/j.envpol.2021.118652.

Wang, L., Lu, P., Feng, S., Hamel, C., Sun, D., Siddique, K.H.M., and Gan, G.Y. (2024b). Strategies to improve soil health by optimizing the plant–soil–microbe–anthropogenic activity nexus. Agric. Ecosyst. Environ. **359**:108750. https://doi.org/10.1016/j.agee.2023.108750.

Wang, L., Guo, S., Hijri, M., Farooq, M., Rehman, A., Ge, T., Feng, S., Wei, Z., Zhang, J.-L., Kang, S., et al. (2025b). Enhancing carbon restoration and ecosystem resilience in global drylands via water-to-carbon biotransformation strategies. Commun. Earth Environ. https://doi.org/10.1038/s43247-025-02874-1.

Wang, L., Garland, G.M., Ge, T., Guo, S., Kebede, E.A., He, C., Hijri, M., Plaza-Bonilla, D., Stringer, L.C., Davis, K.F., et al. (2025c). Integrated strategies for enhancing agrifood productivity, lowering greenhouse gas emissions, and improving soil health. Innovation **6**:101006. https://doi.org/10.1016/j.xinn.2025.101006.

Wang, M., Ge, A.-H., Ma, X., Wang, X., Xie, Q., Wang, L., Song, X., Jiang, M., Yang, W., Murray, J.D., et al. (2024c). Dynamic root microbiome sustains soybean productivity under unbalanced fertilization. Nat. Com **15**:1668. https://doi.org/10.1038/s41467-024-45925-5.

Wanke, A., van Boerdonk, S., Mahdi, L.K., Wawra, S., Neidert, M., Chandrasekar, B., Saake, P., Saur, I.M.L., Derbyshire, P., Holton, N., et al. (2023). A GH81-type 13-glucan-binding protein enhances colonization by mutualistic in barley. Curr. Biol. **33**:5071–5084.e5077. https://doi.org/10.1016/j.cub.2023.10.048.

Wojciechowski, A., Seassau, C., Soerensen, L., Alletto, L., and Lamichhane, J.R. (2023). Effects of cover crops on maize establishment, root mycorrhizal colonization, plant growth and grain yield depend on their botanical family: A global meta-analysis. Agric. Ecosyst. Environ. **356**:e108648. https://doi.org/10.1016/j.agee.2023.108648.

Wu, S., Shi, Z., Chen, X., Gao, J., and Wang, X. (2022a). Arbuscular mycorrhizal fungi increase crop yields by improving biomass under rainfed condition: a meta-analysis. PeerJ **10**:e12861. https://doi.org/10.7717/peerj.12861.

Wu, S., Fu, W., Rillig, M.C., Chen, B., Zhu, Y.-G., and Huang, L. (2024). Soil organic matter dynamics mediated by arbuscular mycorrhizal fungi – an updated conceptual framework. New Phytol. **242**:1417–1425. https://doi.org/10.1111/nph.19178.

Wu, X., Liu, Y., Luo, H., Shang, L., Leng, C., Liu, Z., Li, Z., Lu, X., Cai, H., Hao, H., and Jing, H.C. (2022b). Genomic footprints of sorghum domestication and breeding selection for multiple end uses. Mol. Plant **15**:537–551. https://doi.org/10.1016/j.molp.2022.01.002.

Wu, Y., Deng, M., Huang, J., Yang, S., Guo, L., Yang, L., Ahirwal, J., Peng, Z., Liu, W., and Liu, L. (2022c). Global patterns in mycorrhizal mediation of soil carbon storage, stability, and nitrogen demand: A meta-analysis. Soil Biol. Biochem. **166**:108578. https://doi.org/10.1016/j.soilbio.2022.108578.

Zaman, F., Hassan, M.U., Khattak, W.A., Ali, A., Awad, M.F., and Chen, F.-S. (2024). The pivotal role of arbuscular mycorrhizal fungi in enhancing plant biomass and nutrient availability under drought stress conditions: A global meta-analysis. Sci. Total Environ. **955**:176960. https://doi.org/10.1016/j.scitotenv.2024.176960.

Zárate Martínez, O., Hiiesalu, I., Sepp, S.-K., Koorem, K., Vasar, M., Wipulasena, A.Y.A.P., Liu, S., Astover, A., Öpik, M., Pärtel, M., et al. (2024). Arbuscular mycorrhizal fungal diversity in agricultural fields is explained by the historical proximity to natural habitats. Soil Biol. Biochem. **199**:109591. https://doi.org/10.1016/j.soilbio.2024.109591.

Zayova, E., Stancheva, I., Geneva, M., Hristozkova, M., Dimitrova, L., Petrova, M., Sichanova, M., Salamon, I., and Mudroncekova, S. (2018). Arbuscular mycorrhizal fungi enhance antioxidant capacity of in vitro propagated garden thyme (Thymus vulgaris L.). Symbiosis **74**:177–187. https://doi.org/10.1007/s13199-017-0502-7.

Zhang, C., van der Heijden, M.G.A., Dodds, B.K., Nguyen, T.B., Spooren, J., Valzano-Held, A., Cosme, M., and Berendsen, R.L. (2024). A tripartite bacterial-fungal-plant symbiosis in the mycorrhiza-shaped microbiome drives plant growth and mycorrhization. Microbiome **12**:13. https://doi.org/10.1186/s40168-023-01726-4.

Zhang, H., Liu, Z., Zheng, C., Ma, H., Zeng, M., and Yang, X. (2025). Root system architecture plasticity with beneficial rhizosphere microbes: Current findings and future perspectives. Microbiol. Res. **292**:128028. https://doi.org/10.1016/j.micres.2024.128028.

Zhang, L., Zhou, J., George, T.S., Limpens, E., and Feng, G. (2022a). Arbuscular mycorrhizal fungi conducting the hyphosphere bacterial orchestra. Trends Plant Sci. **27**:402–411. https://doi.org/10.1016/j.tplants.2021.10.008.

Zhang, N., Wang, Z., Shao, J., Xu, Z., Liu, Y., Xun, W., Miao, Y., Shen, Q., and Zhang, R. (2023). Biocontrol mechanisms of *Bacillus*: Improving the efficiency of green agriculture. Microb. Biotechnol. **16**:2250–2263. https://doi.org/10.1111/1751-7915.14348.

Zhang, Q., Koide, R.T., Liu, J., Li, Z., Sun, Z., Sun, Q., and Yang, H. (2022b). Intraspecific plant interaction affects arbuscular mycorrhizal fungal species richness. Plant Soil **470**:141–152. https://doi.org/10.1007/s11104-021-04962-5.

Zhang, Q., Zhu, D., Ding, J., Zheng, F., Zhou, S., Lu, T., Zhu, Y.-G., and Qian, H. (2019a). The fungicide azoxystrobin perturbs the gut microbiota community and enriches antibiotic resistance genes in *Enchytraeus crypticus*. Environ. Int. **131**:104965. https://doi.org/10.1016/j.envint.2019.104965.

Zhang, S., Lehmann, A., Zheng, W., You, Z., and Rillig, M.C. (2019b). Arbuscular mycorrhizal fungi increase grain yields: a meta-analysis. New Phytol. **222**:543–555. https://doi.org/10.1111/nph.15570.

Zhang, X., Dong, W., Sun, J., Feng, F., Deng, Y., He, Z., Oldroyd, G.E.D., and Wang, E. (2015). The receptor kinase *CERK1* has dual functions in symbiosis and immunity signalling. Plant J. **81**:258–267. https://doi.org/10.1111/tpj.12723.

Zhang, Y., Zou, J., Meng, D., Dang, S., Zhou, J., Osborne, B., Ren, Y., Liang, T., and Yu, K. (2020). Effect of soil microorganisms and labile C availability on soil respiration in response to litter inputs in forest ecosystems: A meta-analysis. Ecol. Evol. **10**:13602–13612. https://doi.org/10.1002/ece3.6965.

Zhao, R., Li, X., Bei, S., Li, D., Li, H., Christie, P., Bender, S.F., and Zhang, J. (2021). Enrichment of *nosZ*-type denitrifiers by arbuscular mycorrhizal fungi mitigates N_2O emissions from soybean stubbles. Environ. Microbiol. **23**:6587–6602. https://doi.org/10.1111/1462-2920.15815.