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REVIEW

Fungal highways to water: Mechanisms of drought tolerance in arbuscular and ectomycorrhizal symbioses

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Abstract

Drought is an increasingly important constraint on plant productivity, affecting agricultural yields, forest dynamics, and ecosystem functioning worldwide. Mycorrhizal symbioses formed by arbuscular (AM) and ectomycorrhizal (EcM) fungi are key regulators of plant responses to water limitation, influencing water acquisition, transport, and maintenance of plant water status at the soil–plant interface. This review synthesizes current knowledge of the mechanistic pathways through which mycorrhizal associations enhance plant drought tolerance. We distinguish between direct hydraulic contributions, including expanded soil exploration via extraradical hyphal networks, hyphal water uptake, redistribution, and modifications of rhizosphere hydraulic properties, and indirect physiological and biochemical effects, such as changes in root system architecture, regulation of aquaporins, osmotic adjustment, antioxidant capacity, and phytohormonal signaling. Particular emphasis is placed on structural and functional differences between AM and EcM symbioses. We examine how contrasting intraradical interfaces (i.e., arbuscules versus Hartig net) and extraradical networks influence water movement, plant hydraulic conductance, and whole-plant performance under drought. We assess the implications of these processes for agriculture and forestry, highlighting context-dependent fungal–plant compatibility, maintenance of diverse mycorrhizal communities, and management practices that preserve soil structure and mycorrhizal networks. Despite substantial evidence that mycorrhizal fungi improve plant performance under water deficit, their quantitative contributions to plant water transport and growth remain insufficiently resolved, particularly in EcM-dominated systems. Addressing these knowledge gaps will require integrative, multi-scale approaches linking molecular regulation, root and hyphal hydraulics, and ecosystem-level water fluxes. Such advances are critical for predicting vegetation responses to intensifying drought conditions under global change.

Keywords Arbuscular mycorrhizal fungi · Ectomycorrhizal fungi · Drought tolerance · Hyphal water uptake · Mycorrhizosphere hydraulic properties

Introduction

According to the Sixth Synthesis Report (2023) of the Intergovernmental Panel on Climate Change (IPCC), climate change poses a major threat to terrestrial ecosystems and human well-being, having already reduced food and water security in many regions due to warming, altered rainfall patterns and the increased frequency of extreme events. It also contributes to desertification and exacerbates land degradation, particularly in arid areas and coastal regions (IPCC 2023). The increased frequency, intensity, and duration of droughts have a considerable impact on the agricultural sector, particularly on crops, livestock, forestry, fishing and aquaculture. According to the Food and Agriculture Organization (FAO 2021), agriculture absorbs 63% of the global impact of climate change compared to other sectors.

Over the past 40 years, the total area of terrestrial ecosystems affected by drought has more than doubled, and each year, nearly 12 million hectares of land are lost to desertification (UNCCD 2022). In plants, the impact of

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drought is multidimensional. It causes changes in physiological, morphological, biochemical, and molecular characteristics (Shao et al. 2008; Farooq et al. 2009; Bhargava and Sawant 2013). Yet, plants deploy various defense mechanisms at the cellular and organism levels, such as closing their stomata, developing smaller and succulent leaves to reduce water loss through transpiration, and growing deeper root systems. In addition, osmolytes, including glycine betaine, proline, and other amino acids, play vital roles in maintaining cellular functions during periods of drought (Farooq et al. 2012).

In plant ecophysiology, drought resistance is generally considered an umbrella term encompassing both drought tolerance and drought avoidance strategies (Blum 2005; Verslues et al. 2006). Drought tolerance refers to the ability of plants to maintain physiological functioning under low water availability, whereas drought avoidance involves mechanisms that limit plant water deficit through improved water acquisition or reduced water loss (Verslues et al. 2006). In this context, mycorrhizal fungi may contribute to both drought tolerance and avoidance through their effects on plant water relations and soil water exploration.

In the recent decade, numerous studies have highlighted the role of microorganisms (e.g., bacteria, fungi) that develop in the rhizosphere and root endosphere (i.e. all inner tissues) in reducing plant stress during periods of drought (Poudel et al. 2021). Among the microorganisms that interact with plants, mycorrhizal fungi are of paramount importance, developing as symbionts in the roots of most terrestrial plants in the vast majority of vegetated terrestrial ecosystems (Smith and Read 2008). Four main types of mycorrhizas are recognized, the two main ones globally being the arbuscular mycorrhiza (AM) and ectomycorrhiza (EcM). They have been shown to increase plant tolerance to drought through several mechanisms, but to our knowledge, their specific characteristics and effectiveness have never been compared.

This review aims to compare the roles of AM and EcM fungi[1] in the response of plants to drought stress. Specifically, we aim to (1) highlight the morphological and physiological differences between AM and EcM fungi with respect to water transport; (2) assess the contribution of these two types of mycorrhizas to plant water uptake and the underlying mechanisms; (3) evaluate the effectiveness of AM and EcM fungi in improving plant drought tolerance and (4) discuss future research perspectives and directions for the application of AM and EcM fungi to crops and forests subjected to drought stress.

[1] Species names are reported throughout the manuscript as used in the original publications cited and may not always reflect current taxonomic revisions.

Morphological and physiological properties of mycorrhizal fungi in relation to water transport

Mycorrhizal symbiosis

Evolution

Mycorrhizal fungi are ubiquitous in terrestrial ecosystems, forming symbiotic associations with more than 80% of plant species (Smith and Read 2008). Arbuscular mycorrhiza (AM) are formed by fungi belonging mainly to the Glomeromycota, although some lineages associated with Mucoromycota have also been reported. AM associations occur in most herbaceous plants and in approximately 70–80% of angiosperms worldwide, while being less common among gymnosperms (Tedersoo et al. 2018). Fossils and molecular evidence indicate that AM fungi emerged more than 450 million years ago, contemporaneously with the earliest land plants. The presence of arbuscule-like structures in Ordovician fossils (≈460–470 Ma) suggests that these symbioses played a crucial role in facilitating plant terrestrialization and nutrient acquisition during the early colonization of land (Berbee et al. 2020). The phylum Glomeromycota currently encompasses approximately 370 recognized species (Corradi et al. 2025), a surprisingly low number compared to other fungal groups such as Basidiomycota and Ascomycota (James et al. 2006). This limited species diversity may be attributed to the generally broad compatibility between AM fungi and most vascular plants, which has traditionally been interpreted as reflecting low host specialization (Smith and Read 1997). However, more recent studies suggest a more nuanced view, indicating that host identity and root traits can influence AM fungal community composition and the degree of host specificity (Sepp et al. 2019; Ramana et al. 2023).

With more than 20,000 species (Rinaldi et al. 2008) and more than 80 distinct clades within the Basidiomycota and Ascomycota (and rarely in the Zygomycota), fungi forming EcM symbiosis are the most diverse among fungi forming mycorrhizae (Tedersoo et al. 2010). Despite mycorrhizal associations being prevalent in the majority of plants, EcM fungi are only found in approximately 2% of plant species (Brundrett 2017). Remarkably, this 2% includes the most widespread tree species in forest ecosystems, accounting for approximately 60% of all tree species (Steidinger et al. 2019). Some plants also host AM and EcM fungi. For instance, Teste et al. (2020) identified 211 plant genera within 67 families that have been potentially considered to have a dual-mycorrhizal status. Notably, some plant species are

capable of forming associations with both AM and EcM fungi, either simultaneously or across developmental stages, and such mixed systems have been documented across multiple biomes, particularly in forest ecosystems involving genera such as *Populus*, *Alnus*, *Quercus* and *Eucalyptus*, where both AM and EcM fungi can co-occur within the same root systems or stands (Adjoud-Sadadou and Halli-Hargas 2017; Boeraeve et al. 2019; Teste et al. 2020; Karst et al. 2021; Rog et al. 2025). The evolutionary origins of EcM fungi can be traced back to approximately 180 million years ago, appearing later than AM fungi (Hibbett and Matheny 2009). They independently evolved multiple times, as evidenced by studies conducted by Ryberg and Matheny (2012) and Kohler et al. (2015). The progenitors of EcM fungi are hypothesized to be ecologically diverse decomposer ancestors, as supported by the convergent losses of various components of the ancestral saprotrophic apparatus (Ryberg et al. 2022). Furthermore, the evolutionary diversification and expansion of these fungi are attributed to rapid genetic renewal in symbiosis-induced genes, as elucidated by Kohler et al. (2015).

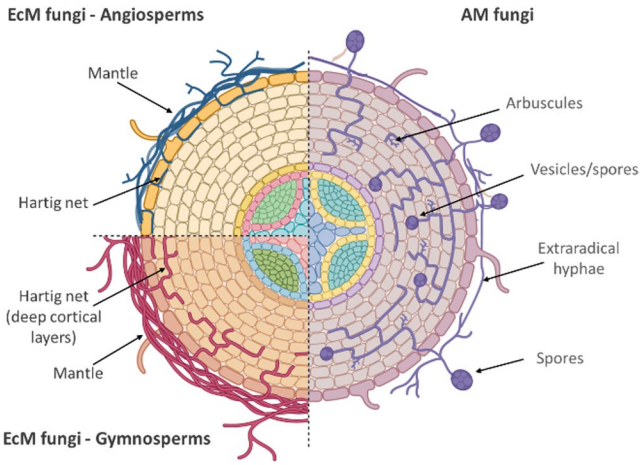

Fig. 1 Structural differences between arbuscular mycorrhizal (AM) and ectomycorrhizal (EcM) symbioses in roots. In AM symbiosis (right), fungal hyphae penetrate cortical cells forming arbuscules, the main sites of nutrient exchange, and vesicles or spores, which function as storage and reproductive structures. Depending on the AM fungal lineage and developmental stage of the symbiosis, intracellular structures may vary, with some AM fungi forming coils instead of arbuscules and some taxa not producing vesicles. AM fungi also develop extraradical hyphae that extend into the surrounding soil forming spores and for some genera (not shown here) auxiliary cells. In EcM symbiosis (left), roots are surrounded by a fungal mantle, and hyphae form an intercellular network known as the Hartig net, where nutrient exchange occurs. In angiosperms, the Hartig net is typically restricted to the epidermis or outer cortical layers, whereas in gymnosperms it commonly extends deeper into the cortex. These structural differences influence the extent of soil exploration and water transport in the two symbiotic types. Created in BioRender. Musella P (2026) https://BioRender.com/yelef7z

Colonization strategies

Mycorrhizal interactions are generally classified according to the anatomical organization of the symbiosis within plant roots. Two major categories are commonly distinguished. The first, ectomycorrhizae (EcM), is characterized by fungal hyphae that remain restricted to the intercellular spaces of the root epidermis and outer cortical tissues, without penetrating host cells. The second, endomycorrhizae, includes arbuscular mycorrhiza (AM), in which specialized fungal structures penetrate the living cortical cells of the host plant (Fig. 1). AM fungal colonization begins with the germination of propagules (mainly spores or vesicles) that have limited independent growth capacity (Hepper 1984). The germinating hyphae then come into contact with the roots, forming a hyphopodium on the epidermal cells (Bonfante and Genre 2010), from which the fungus develops a prepenetration apparatus and colonizes the epidermis and cortex. Depending on the plant–fungus combination, this colonization may lead to the formation of arbuscules, intracellular hyphal coils, or arbusculate coils within the cortical root cells without disrupting the integrity of the plant plasma membrane (Peterson and Bonfante 1994; Dickson 2004). Some genera also produce vesicles/spores within the roots (Redecker et al. 2013). EcM fungi, on the other hand, form a mantle around the roots and a network of intercellular hyphae (i.e., the Hartig net) that intertwine between the epidermal cells of angiosperms and deeper into the cortical cell layers of gymnosperms (Kottke and Oberwinkler 1987; Smith and Read 2008), but never penetrate inside the cells.

Morphological structures

Mycorrhizal fungi possess both intraradical structures inside the roots and an extensive extraradical mycelium (ERM) in the soil, and together these components largely determine their capacity to absorb and transfer water to their host plants.

In AM fungi, a structure putatively involved in water exchange between the partners is the arbuscule, whose highly branched morphology and the periarbuscular membrane maximize the interface for nutrient transfer; this interface also supports bidirectional exchange between the fungal and plant partners (Bonfante-Fasolo 1984; Smith and Smith 1990; Gutjahr and Parniske 2013; Harrison and Ivanov 2017). They also form vesicles and intraradical spores, which contribute to drought tolerance by storing reserves, primarily lipids, that can be mobilized during stress (Smith and Read 2008; Hashem et al. 2019; Sendek et al. 2019). Their extraradical structures consist of fine, aseptate hyphae and branched absorbing structures (BAS) that form dense, interconnected networks that potentially facilitate plant

access to water under drought conditions (Bago et al. 1998; Giovannetti et al. 2001, 2006, 2015; Allen 2007).

In EcM fungi, the principal intraradical structure is the Hartig net, a highly branched intercellular hyphal network in the root apoplast that constitutes the main exchange interface for nutrient transfer between fungus and host and is thought to play an important role in water exchange and plant water relations (Lehto and Zwiazek 2011; Nehls and Plassard 2018; Stuart and Plett 2020). Their extraradical structures range from dense hyphal mats to long-distance rhizomorphs equipped with vessel hyphae and protective layers, enabling efficient water translocation (Eamus et al. 1985; Agerer 2001, 2006; Newton 1992, 2007; Read 1991; Yafetto et al. 2009; Fernandez and Koide 2013). Overall, AM fungi rely on thin, continuous hyphae that may contribute to plant water acquisition from soil microsites, whereas EcM fungi exploit reinforced rhizomorphs and the Hartig net to transport water over greater distances.

Contribution of AM and EcM fungi to plant drought tolerance

Mycorrhizal fungi improve plant drought tolerance through two complementary categories of mechanisms: direct mechanisms, in which the fungus itself contributes to plant's acquisition of water, and indirect mechanisms, in which the symbiosis improves plant performance during periods of drought without direct water transport.

Direct mechanisms – These functions include the extension of the soil exploration zone through the development of extensive extraradical mycelial networks and specialized hyphal structures that uptake and transport (Leake et al. 2004), including (1) dense and broad extraradical hyphae, where AM fungal networks can reach densities of 2.7–20.5 m g^{-1} of soil and EcM fungal rhizomorphs can extend several meters from the roots in the soil (Giovannetti et al. 2006; Allen 2007), (2) the penetration of fine soil pores containing water inaccessible to roots (Allen 2007), (3) the structural adaptations of hyphae such as hydrophobic cell walls and vessels hyphae facilitating long-distance water movement (Agerer 2006; Yafetto et al. 2009), (4) the formation of common mycorrhizal networks capable of redistributing water between plants (Egerton-Warburton et al. 2007; Warren et al. 2008), and (5) the direct uptake and translocation of water through hyphal pathways (Khalvati et al. 2005; Ruth et al. 2011; Duddridge et al. 1980). These structural differences and their implications for water transport are summarized in Fig. 2.

Indirect mechanisms – They improve plant drought tolerance by enhancing physiological, biochemical, and structural resilience, while simultaneously modulating soil hydraulic properties and water availability through their effects on soil structure and the development of extraradical mycelial networks (Augé et al. 2001; Querejeta 2017). This includes (1) the increased soil aggregation and water retention mediated by glomalin or hydrophobins (Rillig et al. 2003; Hallett 2008; Hallett et al. 2009), (2) the modifications of root architecture that expand the absorptive interface or alter root hair traits (Gutjahr and Paszkowski 2013; Felten et al. 2009), (3) the improved nutrient acquisition under drought—particularly P for AM fungi and organic N for EcM fungi (Harrison and van Buuren 1995; Bödeker et al. 2014)—as well as the regulation of plant aquaporins (Marjanović et al. 2005; Aroca et al. 2008; Xu et al. 2016), (4) the improvement of the photosynthesis and stomatal conductance (Yano-Melo et al. 1999; Wang et al. 2021), (5) the modulation of drought-related phytohormones such as abscisic acid (ABA) and jasmonic acid (JA) (Aroca et al. 2008; Luo et al. 2009), and (6) the activation of antioxidant systems that limit reactive oxygen species damage (Bitaraf et al. 2020; Alvarez et al. 2009). Because these processes operate simultaneously at multiple organizational levels, from soil to canopy, a schematic overview is provided to summarize the main indirect mechanisms involved (Fig. 3).

Together, these direct and indirect mycorrhizal-mediated mechanisms improve plant survival and performance during drought, although their relative contributions vary depending on the type of fungi, plant species, and environmental conditions.

Direct mechanisms

Volume of soil explored

The external hyphae of some AM fungi can extend several tens of centimeters from the root surface. Assuming a radial distribution of hyphae around roots, the volume of soil explored by a root system colonized by AM fungi can be up to 100 times greater than that explored by a non-colonized root system (Sieverding 1991). By extending the effective absorptive surface beyond the rhizosphere, AM fungal hyphae may attenuate the decline in matric potential near the root surface during soil drying (Abdalla et al. 2023). The ERM network of AM fungi exhibits a high degree of interconnectivity through hyphal fusions, corresponding to approximately 5 to 150 anastomoses per meter of hyphae (Giovannetti et al. 2006, 2015). ERM length in soil ranges from 2.7 to 20.5 m g^{-1} of soil, with a mean growth rate of 0.74 to 1.1 m day^{-1} and a specific hyphal weight of 3.8 to 7.8 µg m^{-1} (Giovannetti et al. 2001, 2006). This corresponds to an absorbing surface area of approximately 0.3 to 2.6 cm^2 g^{-1} soil, assuming an

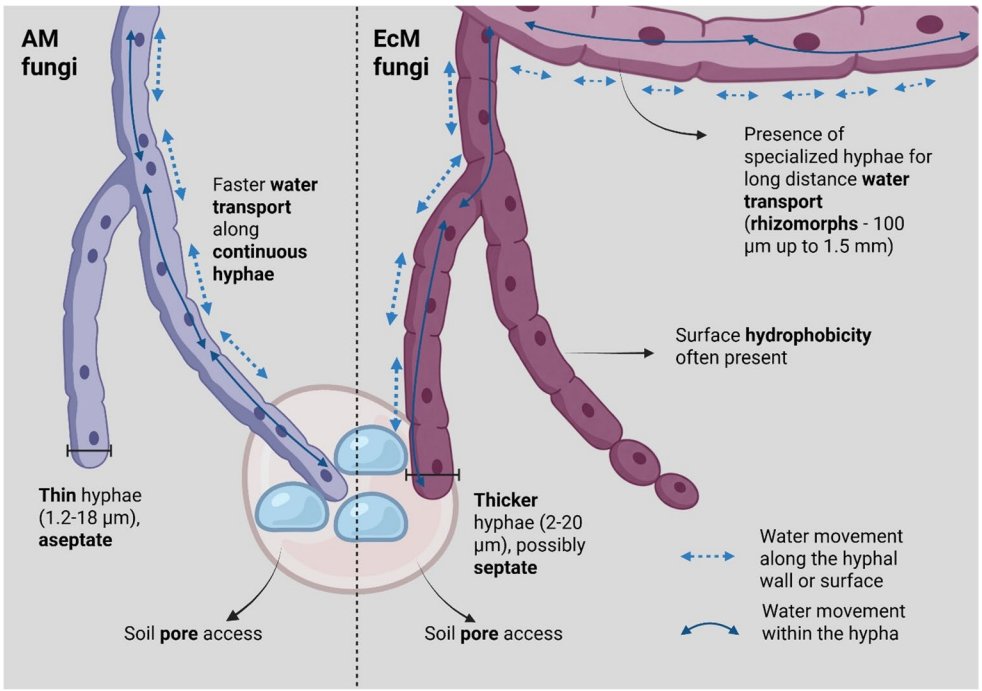

Fig. 2 Structural traits of arbuscular mycorrhizal (AM) and ectomycorrhizal (EcM) fungal hyphae underlying direct water transport mechanisms. AM fungi produce thin, aseptate hyphae that enable access to soil micropores and facilitate rapid water movement along continuous hyphal pathways. In contrast, EcM form thicker, often septate hyphae and specialized rhizomorphs capable of long-distance hydraulic transport and exhibiting surface hydrophobicity, which affects water flow dynamics. Light blue arrows represent the direction of water movement through fungal structures toward the host plant and viceversa. Together, these anatomical differences illustrate the distinct hydraulic strategies of AM and EcM fungi that may contribute directly to plant water uptake during drought. Created in BioRender. Musella P (2026) https://BioRender.com/l2sqlfa

average hyphal diameter of 4 µm. These structural characteristics may influence water uptake capacity, as AM fungal hyphae have been shown to mediate the flow of molecules from soil to host roots, improving plant growth and nutrient status (Avio et al. 2006). Recent studies further demonstrated that the AM fungal ERM is a dynamic and highly coordinated network composed of functionally differentiated hyphal structures, including runner hyphae involved in long-distance transport and BAS associated with nutrient uptake zones (Bago et al. 1998 c; Kokkoris 2026). Moreover, AM fungal network expansion appears to emerge from self-organized wave-like growth dynamics coupled with frequent hyphal self-fusions that reinforce network connectivity and resource translocation efficiency (Oyarte Galvez et al. 2025; Kokkoris 2026).

EcM fungi also develop extensive ERM, and their soil-exploration strategies are highly diverse (Leake et al. 2004). Although EcM fungal hyphae are more difficult to distinguish morphologically from saprotrophic fungi, making hyphal length estimates less reliable, available data suggest densities ranging from 3 to 600 m g^{-1} of soil (Jones et al. 2009). Some fungi, like *Cenococcum* spp., form localized but dense hyphal networks, while others, such as *Pisolithus* spp., develop complex cords that can extend several meters from the root system to access water patches (Agerer 2001; Allen 2007). These fungi also produce rhizomorphs, fungal structures with an elongated, cord-like appearance, distinct from regular mycelial hyphae (Allen 1991). Composed of densely packed fungal hyphae, rhizomorphs have a reinforced structure that facilitates resource transport (e.g. water and nutrients). In DNA-based mapping studies, the ERM of some EcM fungal species (e.g., *Hebeloma cylindrosporum*) has been detected 40 cm away from the root or fruiting bodies, suggesting a patchy, spatially heterogeneous distribution in soil (Guidot et al. 2002). It may be worth considering that more extensive soil exploration does not necessarily imply better plant performance under drought conditions. For example, García de Jalón et al. (2020) demonstrated that the relative abundance of short and medium-range exploration types increased seedling survival, while other authors found that the relative abundance of medium and long-range exploration types decreased tree growth, possibly due to a greater C input required for mycelium production (Anthony et al. 2022). However, contrasting evidence exists, as recent experimental work showed that seedlings surviving drought were enriched in ectomycorrhizal fungi with

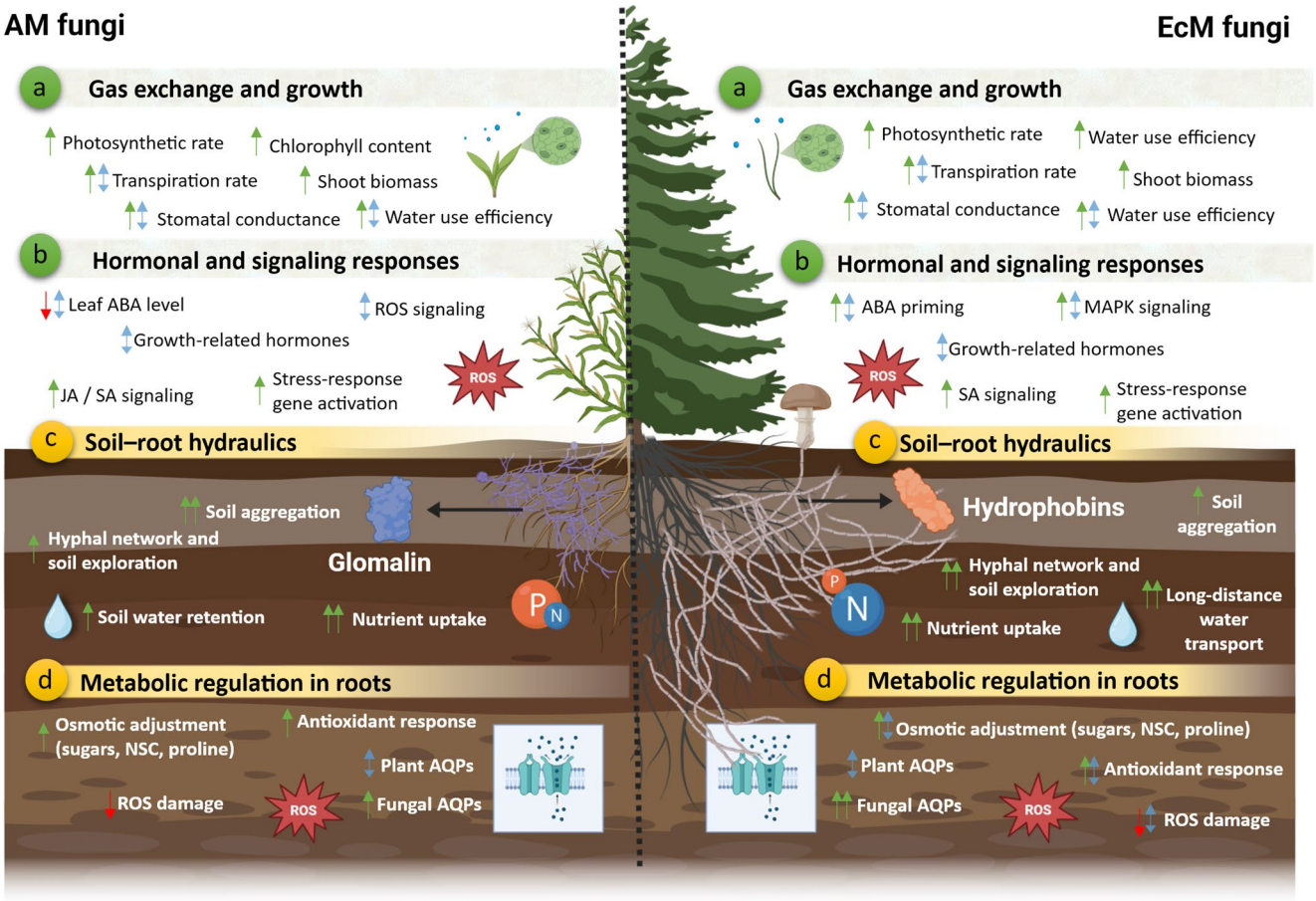

Fig. 3 Indirect mechanisms by which arbuscular mycorrhizal (AM) and ectomycorrhizal (EcM) fungi enhance plant performance under drought conditions. Indirect effects of mycorrhizal symbiosis are shown separately for AM fungi (left) and EcM fungi (right). Mechanisms are grouped into aboveground and belowground processes. (**a**) gas exchange and growth, including changes in photosynthetic rate, transpiration, stomatal conductance, chlorophyll content, water-use efficiency, and shoot biomass; (**b**) hormonal and signaling responses, including modulation of abscisic acid (ABA), jasmonic and salicylic acid (JA/SA), growth-related hormones, reactive oxygen species (ROS) signaling, and activation of stress-response pathways such as mitogen-activated protein kinase (MAPK) cascades.; (**c**) soil–root hydraulics and nutrient uptake, driven by hyphal networks, soil exploration, soil aggregation mediated by glomalin in AM fungi or hydrophobins in EcM fungi, and regulation of plant and fungal aquaporins; and (**d**) metabolic regulation in roots, including osmotic adjustment (e.g., soluble sugars, non-structural carbohydrates, and proline) and antioxidant responses that help limit oxidative damage under drought stress. Arrows indicate trends reported in the literature: ↑ increase, ↑↑ strong and consistently documented increase, ↓ decrease, and ↕ variable responses depending on plant species, fungal taxa, and environmental conditions. Symbols ↑↕ and ↓↕ indicate responses that are frequently reported as increases or decreases, respectively, but remain context-dependent. Created in BioRender. Musella P (2026) https://BioRender.com/7gotkb9

long exploration types, hydrophobic mycelia and rhizomorphs, traits potentially associated with improved water transport efficiency (Castaño et al. 2023).

The depth distribution of AM and ECM fungi is closely linked to the vertical extension of the roots of their host plants. Root colonization by AM fungi has been observed down to 8 m in eucalyptus and acacia plantations (Sosa-Hernández et al. 2019), while colonization by EcM fungi has been found at least 4 m deep in the fine roots of eucalyptus plantation in Brazil (Robin et al. 2019). Their ability to access water at such depths remains unresolved, although deep ectomycorrhizal hyphae and rhizomorphs have been proposed as potential pathways connecting plants to water stored in deep weathered bedrock and soil micropores (Bornyasz et al. 2005).

In summary, both AM and EcM fungi develop extensive ERM networks that greatly enhance soil exploration, using various structural strategies—from the dense, interconnected hyphae of AM fungi to the highly specialized, long-distance rhizomorphs of EcM fungi — to improve water acquisition for the host plant.

Soil pores exploration

Mycorrhizal hyphae are able to penetrate soil pores and rocks thanks to several unique characteristics. First, they

are extremely thin and can grow into soil pores as small as 2 µm (Allen 2007). The external diameter of AM fungal hyphae has been measured between 1.2 and 18 µm (e.g., Dodd and Ruiz-Lozano 2012). The same is true for EcM fungal hyphae, whose diameter ranges from 2 to 20 µm for the finest hyphae (Allen 2007), while rhizomorphs can reach 100 µm or even 1.5 mm in diameter (Freymann 2008). For comparison, the diameter of root hairs generally varies from 10 to 20 µm (Wulfsohn and Nyengaard 1999; Grierson et al. 2014), and that of fine roots typically ranges between 50 and 2000 µm (Pierret et al. 2005). This small size allows hyphae to access niches physically inaccessible to roots.

Due to their filamentous shape at the micrometric scale, the hyphae of AM and EcM fungi occupy several meters of pore space in a single cubic centimeter of soil (Godbold et al. 2006).

Hyphae structure and water uptake in soil

EcM fungi can be broadly classified based on the predominant hydrophobicity of their extraradical structures, with many taxa producing hydrophobic mycelial aggregates, while other taxa develop mainly diffuse hydrophilic mycelium adapted to humid or water-saturated soils (Unestam and Sun 1995). From a functional perspective, hydrophilic EcM hyphae primarily facilitate water uptake and short-distance transport via capillary flow along the hyphal surface and within the cell wall, whereas hydrophobic hyphae restrict surface-mediated flow and instead favor internalized water transport within the hyphal lumen or specialized conducting structures (Unestam and Sun 1995; Allen 2007). Hydrophobicity is not necessarily uniform within a single mycelial system. The same EcM fungus can produce functionally differentiated structures (i.e. fine exploratory hyphae and aggregated rhizomorphs), which may differ in surface properties. In addition, hydrophobicity can vary along individual hyphae, reflecting developmental stage and local differences in wall or surface composition, with younger or actively growing regions differing from older, more differentiated parts (Unestam and Sun 1995). These differences are largely associated with variations in surface composition and extracellular coatings, including hydrophobins, extracellular matrices, and other compounds (e.g. polysaccharides, melanins, and glycoproteins), which can differ among hyphal types and developmental stages, allowing a single EcM fungus to express distinct surface properties across the mycelium (Unestam and Sun 1995; Wösten 2001). Unestam (1991) suggested that the hydrophobic property of many forest mycorrhizae was an ecological adaptation to the periodically dry conditions that are often typical of the upper soil layers of the boreal forest. This unique morphology enables them to extend cover greater distances in the soil and reflects ectomycorrhizal exploration strategies associated with resource acquisition and transport (Read 1991; Read and Boyd 1986; Agerer 2001). Composed of densely aggregated hyphae, rhizomorphs exhibit a reinforced, functionally differentiated structure that facilitates long distance water transport and nutrient exchange (Brownlee et al. 1983; Agerer 2001). They often feature a protective outer layer, which can be melanized, like in *Cenococcum geophilum*, to shield against environmental stressors like desiccation (Fernandez and Koide 2013). Internally, rhizomorphs develope a central cavity, surrounded by a layer of thin-walled hyphae known as vessel hyphae. Vessel hyphae allow the easy passage of water and osmolytes across the wall surface (Yafetto et al. 2009). Eamus et al. (1985) demonstrated that long-distance translocation in mycelial cords and rhizomorphs occurs predominantly through solution flow along vessel hyphae, thereby supporting the bidirectional transport of water and solutes between the soil and the host plant.

Amyloid hyphal walls or septa occur in hyphae of rhizomorphs of several EcM fungal species (Agerer 2006). They can present trumpet-like structures below the septum of the hypha, which may play a role as a temporary storage of nutrients and water before they are needed for growth or transferred to the host. Ampullate hyphae are frequent in EcM fungi and are extraordinarily efficient in water extraction (Agerer 2006). Even if the external hyphae of rhizomorphs can be septate, an aseptate lumen is required for the movement of nutrients and water in mass within the vessel hyphae towards the rhizomorph tip (Yafetto et al. 2009).

In contrast, AM fungal hyphae do not form chords or rhizomorphs but they can form wrapping “networks” of two to five hyphae extending a few centimeters into the soil (Allen 2006). AM fungal hyphae are characterized by the absence of septa. These hyphae lack the cell wall partitions that delineate compartments, resulting in an uninterrupted conduit for water transport. In addition, as mentioned above, the extraradical mycelium of AM fungi can form BAS, consisting of highly branched, fine hyphae with a large surface-to-volume ratio, which have been proposed as preferred sites for resource uptake and transfer within the mycelial network (Bago et al. 1998). Although AM fungal hyphae can contribute to plant water acquisition, the quantitative importance of direct hyphal water transport remains a matter of debate and may be relatively small compared with plant transpiration demands, suggesting that indirect effects on soil hydraulic properties and root–soil interactions may also play major roles (George et al. 1992; Smith et al. 2010; Püschel et al. 2020).

In summary, many studies have highlighted the crucial role of AM fungal hyphae in water uptake, while observations of mycelial density and structure reveal major differences between AM and EcM fungi. Furthermore, the

presence of BAS and the contrast between hydrophobic and hydrophilic EcM fungal hyphae further underscore the complexity of the adaptations and ecological niches of these fungal communities.

Water distribution by AM and EcM fungi via common mycorrhizal networks

During drought, host plants may transfer hydraulically lifted or redistributed water from deeper soil or bedrock layers to associated AM and EcM fungal symbionts, thereby helping maintain the integrity and functionality of extraradical mycelial networks in dry upper soil horizons (Querejeta et al. 2003; Egerton-Warburton et al. 2008; Lilleskov et al. 2009). This bidirectional water exchange between roots and fungal hyphae may sustain mycorrhizal activity during prolonged drought and could subsequently influence the redistribution of water among neighboring plants through common mycorrhizal networks (CMN) (Dluhosch et al. 2026). AM and EcM fungi can both interconnect plants via CMN (He et al. 2003). Egerton-Warburton et al. (2007) demonstrated that the CMN of AM and EcM fungi can transfer water between plants. For example, fluorescent tracer dyes and deuterium-enriched water were used to follow the pathways of water transfer from oak seedlings (*Quercus agrifolia*) colonized by EcM and AM fungi into the roots of water-stressed seedlings of the same species, or other plant species (*Eriogonum fasciculatum*, *Salvia mellifera*, *Keckiella antirrhinoides*) in the study of Egerton-Warburton et al. (2007). The amount of water was found to be higher in EcM hyphae compared to AM fungal hyphae. EcM hyphae, particularly those produced by certain fungal species such as *Boletus*, *Cortinarius*, and *Pisolithus*, have rhizomorphs that can transport and hold significant amounts of water (Duddridge et al. 1980; Cairney 1991; Agerer 2001, 2006). On the other hand, AM fungal hyphae, such as those produced by *Rhizophagus* and *Scutellospora*, may form large interconnected networks (Hart and Reader 2002) that could facilitate water movement through extensive hyphal continuity and interconnectivity (Giovannetti et al. 2004). However, dye tracer data indicated that water transfer in EcM systems relied on specialized rhizomorph-based pathways, whereas AM-mediated transfer appeared to depend more on dense hyphal networks and host dependence, highlighting contrasting mechanisms of hyphal water movement. Warren et al. (2008) successfully tested the hypothesis that native EcM fungi associated with *Pinus ponderosa* could also transfer water from large trees to seedlings via CMN. Mesh chambers excluding roots but allowing fungal hyphae and rhizomorphs were used, with isotopically labeled water applied to large tree stumps to create a water potential gradient. Within three days, labeled water was detected in the foliage of seedlings more than one meter away, and after three weeks, eight out of ten stemwood samples from seedlings showed significant enrichment, suggesting that EcM fungal hyphae could facilitate direct water transport between large trees and seedlings via the CMN, potentially providing a more efficient hydraulic link for water redistribution than traditional soil pathways. Regarding AM fungi, it is uncertain if adult plants are able to transfer water to seedlings via CMN, as direct evidence is limited and appears mainly context- and species-dependent (Egerton-Warburton et al. 2007; Singh et al. 2019; Püschel et al. 2020; Russell et al. 2025; Bücking et al. 2016).

Water uptake by hyphae

Mycorrhizal symbiosis can alter the movement of water through the plant, thereby changing tissue hydration and leaf physiology (Ruiz-Lozano 2003; Lehto and Zwiazek 2011). Recent evidence suggests that hydraulic limitations during soil drying arise predominantly below-ground, particularly at the soil–root interface and outside-xylem compartments, rather than being driven exclusively by xylem embolism (Carminati and Javaux 2020; Abdalla and Ahmed 2021; Abdalla et al. 2023). In this context, mycorrhizal fungi may play an important role in maintaining hydraulic continuity and regulating water fluxes across the soil–plant continuum under drought conditions.

AM fungi operate precisely at the root–soil interface, which is increasingly recognized as a major hydraulic bottleneck during drought progression (Abdalla et al. 2023). The first evidence of increased water uptake in AM-colonized plants dates back to the 1990s. Faber et al. (1991) on sunflower and cowpea, and Ruiz-Lozano and Azcón (1995) on lettuce, demonstrated an active role of hyphae in water and nutrient transport compared to non-colonized plants. For several years, however, this effect was mainly attributed to changes in root hydraulic conductivity through nutrient supply (Augé 2001). It was only later that the direct contribution of AM fungal hyphae to water uptake by roots was quantified. Using a split-root hyphae system, Khalvati et al. (2005) showed that, in comparison to the control treatment, 4% of the water in the hyphal compartment was transferred to the root compartment through the AM fungal hyphae under drought conditions. Subsequently, Ruth et al. (2011) reported that hyphae contributed at least 20% of total water uptake using high-resolution soil water content sensors, and provided the first estimate of water flux density in hyphae ($22.8\ \mu L\ cm^{-2}\ day^{-1}$).

Water movement through fungal hyphae can occur via two distinct pathways: a symplastic pathway, mediated by aquaporins (AQPs) and intracellular transport processes, and an apoplastic pathway, in which water moves

through the hyphal wall matrix and along the external hyphal surface (Kakouridis et al. 2022). More recently, strong evidence has accumulated for extracytoplasmic water transport in hyphae (Kakouridis et al. 2022). Nevertheless, cytoplasmic transport cannot be ruled out, since AQPs present in both plants and AM fungi may facilitate water flow at the interface between fungal and plant membranes (Aroca et al. 2007, 2009; Maurel et al. 2008; Li et al. 2013). In addition to these mechanisms, the capacity of hyphae to take up water increases under drought, through a combination of enhanced AQPs-mediated membrane permeability, osmotic adjustment that maintains favorable water potential gradients, and structural modifications of the extraradical mycelium that improve access to residual soil water (Aroca et al. 2007, 2009; Allen 2007; Ruiz-Lozano et al. 2012; Kakouridis et al. 2022). Zhang et al. (2018) showed that the hyphal water absorption rate of *Funneliformis mosseae* and *Paraglomus occultum* colonizing citrus (*Poncirus trifoliata*) ranged from 0.607 to 1.973 mg H_2O h^{-1} and 0.126–0.963 mg H_2O h^{-1} per mm of hyphal length, respectively, and that drought stress elevated this rate by 225% and 664%, respectively. Furthermore, Carminati et al. (2023) calculated the hydraulic conductance of AM fungi (assuming 20 m of hyphae per gram of soil and a root length density of 2 cm cm^{-3}) and obtained a value of 3.9×10^{-6} m s^{-1} MPa^{-1}, suggesting that a significant flow through the hyphae can occur, particularly in coarse soils.

For EcM fungi, water transport through the extraradical mycelium has also been clearly demonstrated. Duddridge et al. (1980) showed that the ERM of EcM can deliver water to the host plant. Boyd et al. (1986) demonstrated that this contribution can determine seedling survival under dry conditions in *Suillus bovinus–Pinus sylvestris* association. In this study water transfer was quantified through the translocation of tritiated water (e.g. water in which one or both hydrogen atoms have been replaced by the radioactive isotope tritium), which reached needles 27 cm from the source in an hour, but only when a rhizomorph connected the seedling to the water source, at rates comparable to xylem transport. Further evidence was provided by Brownlee et al. (1983), who showed that *P. sylvestris* seedlings confined to a dry peat zone could only access water through *S. bovinus* mycelial strands crossing into a moist compartment. Seedlings remained alive for almost 10 weeks when the mycelium was the only source of water transport, whereas they lost colour and died within one week when the mycelial strand was severed. Similarly, Muhsin and Zwiazek (2002) showed that seedlings colonized by EcM fungi possessed a smaller root surface area compared to non-mycorrhizal seedlings and provided evidence that the extraradical mycelium and the hyphal net play an important role in water uptake and transport to the host.

Water moves in the fungal symplasm when hyphae absorb water from the soil (Lehto and Zwiazek 2011). While AM fungi penetrate plant cells, EcM fungi form a Hartig net that occupies the intercellular space; consequently, water may need to cross more membranes in EcM-colonized roots, potentially causing a loss of water potential (Lehto and Zwiazek 2011). However, despite this theoretical limitation, many studies have reported that EcM strands increase root hydraulic conductivity (Lamhamedi et al. 1992; Muhsin and Zwiazek 2002; Bogeat-Triboulot et al. 2004; Yi et al. 2008; Wang et al. 2021). Proposed mechanisms include fungal AQP activity (Marjanović et al. 2005; Xu and Zwiazek 2020), increased apoplastic water transport (Muhsin and Zwiazek 2002), and modified water flux in the apoplastic region where nutrient and water exchange occurs (Javot and Maurel 2002; Marjanović et al. 2005; Dietz et al. 2011; Navarro-Ródenas et al. 2013; Xu et al. 2016; Calvo-Polanco et al. 2019). Nonetheless, some studies have reported negative or negligible effects of EcM fungi on root hydraulic conductance, suggesting that the outcome of the symbiosis may depend on both fungal identity and abiotic factors such as soil moisture and temperature (Muhsin and Zwiazek 2002; Kennedy and Peay 2007). Furthermore, EcM and AM fungi are themselves sensitive to soil desiccation, although their vulnerability may differ substantially between mycorrhizal types (Gehring et al. 2006; Querejeta et al. 2009). This intrinsic susceptibility may strongly influence the functioning and overall outcome of the mycorrhizal symbiosis for host plants under drought conditions (León-Sánchez et al. 2018). Finally, the severity and duration of drought are also likely to determine the capacity of mycorrhizal associations to maintain hydraulic functionality and confer drought resilience to host plants (Querejeta et al. 2009).

In conclusion, although AM and EcM fungi rely on distinct structural organizations and transport pathways, both groups possess hyphal mechanisms capable of enhancing plant water uptake, especially under drought conditions.

Indirect mechanisms

Photosynthesis and leaf transpiration

Drought stress reduces photosynthesis through multiple, interconnected mechanisms, including stomatal closure that limits CO_2 availability, disruptions in photochemical processes, and metabolic constraints affecting carbon fixation (e.g., decreased enzyme activities and electron transport) (Fig. 3a) (Wang et al. 2018; Qiao et al. 2024). At the biochemical level, drought stress progressively impairs photosynthesis through metabolic limitations, including reduced

activity and activation state of ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO), impaired RuBisCO regeneration and adenosine triphosphate (ATP) synthesis, and enhanced chlorophyll degradation (Flexas and Medrano 2002; Dalal and Tripathy 2012; Tang et al. 2022). However, under drought conditions Abdel-Salam et al. (2018) showed that AM fungi significantly boost chlorophyll levels, maintain RuBisCO synthesis, and increase the photosynthetic rate. Numerous studies have shown that plants colonized by AM fungi maintain higher rates of photosynthesis and transpiration, have better nutrient and water uptake, and exhibited increased stress tolerance compared to non-mycorrhizal plants. These effects are particularly pronounced under drought stress conditions (Augé 2001; Porcel and Ruiz-Lozano 2004; Zhu et al. 2012). However, the magnitude and direction of mycorrhizal effects on plant water relations and gas exchange remain strongly context dependent, varying according to fungal identity, host species, environmental conditions, drought severity, and the balance between symbiotic costs and physiological benefits (Johnson et al. 1997; Hoeksema et al. 2010; Püschel et al. 2020).

In addition to increasing photosynthetic activity and stomatal conductance, mycorrhizal fungi may under certain conditions enhance intrinsic water use efficiency by differentially modulating carbon assimilation and stomatal conductance under drought conditions (Querejeta et al. 2006). In the research of Yano-Melo et al. (1999), micropropagated banana plantlets (*Musa* spp. cv. 'Pacovan') inoculated with the AM fungi *Acaulospora scrobiculata*, *Glomus clarum* or *Glomus etunicatum* exhibited higher stomatal conductance and a 60–86% increase in transpiration rate relative to non-mycorrhizal controls under well-watered acclimatization conditions, likely reflecting enhanced water uptake capacity and gas exchange rather than improved water conservation. These gains were particularly evident in banana plantlets colonized by *A. scrobiculata*. Enhanced gas exchange and photosynthetic performance in mycorrhizal plants have also been associated with improvements in the ratio of variable to maximum chlorophyll fluorescence (Fv/Fm), which reflects the potential quantum efficiency of Photosystem II. Similar results were found for EcM fungi under drought conditions. *Paxillus involutus* has been shown to significantly increase the rate of photosynthesis and water-use efficiency in *Pinus sylvestris* seedlings under drought conditions (Musella et al. 2025). Similarly, in the experiment of Wang et al. (2021), *Pinus tabulaeformis* inoculated with *S. variegatus* under moderate and severe drought had a significant increase in stomatal conductance, transpiration rate, and photosynthetic rate. The observed effects suggest that *S. variegatus* is involved in the hydraulic adjustments of plants in water deficit situations. High stomatal conductance under low soil moisture conditions may be a consequence of water extraction from the soil by the mycorrhizal association or of the extension of the hyphal exploration area (Duan et al. 1996). Concurrently, higher stomatal conductance can increase CO_2 uptake and the photosynthetic rate (Augé et al. 2015; Gehring et al. 2017). Dosskey et al. (1990) reported that EcM colonization of Douglas-fir seedlings was associated with higher net photosynthetic rates compared with non-mycorrhizal controls, and interpreted this as consistent with the idea that enhanced carbon sink demand by the fungal partner can alleviate feedback inhibition of photosynthesis (i.e., the down-regulation of photosynthetic carbon fixation caused by carbohydrate accumulation in source leaves), thereby helping to maintain carbon assimilation under stress.

Together, these findings indicate that AM and EcM fungi enhance photosynthetic performance under drought by maintaining stomatal function and facilitating carbon balance, thus helping plants maintain their physiological activity when water availability is limited.

Phytohormones regulation

Under drought stress conditions, mycorrhizal associations can induce the activation of various signaling pathways (Fig. 3b), particularly those of plant hormones such as cytokinins, gibberellins, ethylene, ABA, auxins, and JA (Ludwig-Müller 2000). These hormones play a role in the plant's response to drought by regulating their water relationships (Wolters and Jürgens 2009). Recent syntheses indicate that AM fungal symbiosis reshapes drought responses through coordinated hormonal crosstalk, particularly involving ABA, auxins, cytokinins and gibberellins, integrating stress signaling with root development and water-use regulation rather than acting through isolated hormone pathways (Chandrasekaran et al. 2025).

Among the hormones, ABA is the most crucial in coordinating the plant's response to drought (Zhang et al. 2006; Ton et al. 2009). ABA primarily regulates the plant's water status by controlling the opening and closing of stomata through the modulation of guard cell turgidity when the soil becomes dry (Wilkinson and Davies 2010). Fine roots produce ABA, which is then transported upward through the transpiration stream to the stomata guard cells, leading to stomatal closure (Lim et al. 2015). Additionally, ABA activates genes encoding enzymes and proteins involved in cellular dehydration tolerance (Bray 2002; Xiong and Zhu 2003). The impact of AM fungal colonization on ABA levels has been observed in various plant species, particularly during drought, such as tomato (*Solanum lycopersicum*), corn (*Zea mays*), lettuce (*Lactuca sativa*), chile ancho pepper (*Capsicum annuum*), and cowpea (*Vigna unguiculata*) (Duan et al. 1996; Estrada-Luna and Davies

2003; Herrera-Medina et al. 2007; Aroca et al. 2008; Kandowangko et al. 2009; Ruiz-Lozano et al. 2009). Numerous studies have shown that under drought conditions, AM fungi colonization can alter leaf ABA levels in plants compared with non-mycorrhizal controls; in some case ABA is lower in AM-associated leaves, possibly reflecting reduced drought stress perception in the host (Chitarra et al. 2016; Ouledali et al. 2019; Tekaya et al. 2022). The findings of Ouledali et al. (2019), in particular, suggest that AM fungal-colonization impacts stomatal functioning in olive trees under drought conditions. This study showed that stomatal closure was not primarily regulated by ABA, the key hormone controlling stomatal behavior under drought conditions in mycorrhizal olive trees. Instead, other factors related to AM fungi played a role in stomatal regulation in mycorrhizal olive plants exposed to severe drought. These factors likely include improvements in plant water status and root hydraulic conductance induced by AM fungi, leading to stomatal regulation driven by hydraulic signals rather than by ABA accumulation, potentially complemented by enhanced potassium nutrition affecting guard cell functioning.

EcM fungi also appear to be regulators of plant hormonal responses during periods of drought, although current knowledge remains limited. Some studies have shown reductions in ABA content under osmotic stress in EcM-colonized plants (Rincón et al. 2005). In contrast, other studies demonstrated a priming effect to drought induced by EcM fungi, which led to an increase in stress-related hormone contents, ABA and salicylic acid (SA), in poplar trees (*Populus* spp.), even when drought conditions were not present, indicating an anticipatory effect (Luo et al. 2009). In this context, priming refers to a physiological state in which prior symbiotic interaction prepares the plant for enhanced and faster stress responses upon subsequent exposure to stress. Calvo-Polanco et al. (2019) discovered that root colonization by *Laccaria bicolor* affects the response of poplar trees to drought stress by regulating ABA and AQP levels. The study used a split-root system to examine the role of the EcM fungus in plant water relations and hormonal balance under mild drought. The results showed that the presence of *L. bicolor* within the roots down-regulated certain AQPs and specifically reduced the abundance of AQPs of the PIP2 subfamily, considered to be the main pathway for cell-to-cell water transport (Kaldenhoff and Fisher 2006). In addition, fungal AQPs were found to be positively correlated with root ABA content.

In summary, AM and EcM fungi influence drought-related hormonal pathways, shaping stomatal behavior and water transport processes which ultimately enhance plant tolerance in the face of limited water availability.

Root architecture influenced by AM and EcM fungi

While the role of AM and EcM fungi in increasing plant growth through better nutrient and water absorption is well known, they also modulate root architecture in a way that directly influences water uptake efficiency (Table 1) (Hetrick 1991; Atkinson et al. 1994; Cruz et al. 2004; Yao et al. 2009; Gutjahr and Paszkowski 2013; Cockerton et al. 2020). According to Gutjahr and Paszkowski (2013), AM fungi modify root morphology primarily by decreasing the meristematic activity of root apices while promoting the proliferation of lateral roots, thereby increasing root absorption surface area and improving access to water in the soil matrix. This architectural change allows plants to explore a larger volume of soil, thus optimizing water uptake under limiting conditions. However, as Hetrick (1991) noted, in some highly mycotrophic species, AM fungal colonization can inhibit fine root branching, as these plants reduce their own root investment and rely more heavily on the ERM for water and nutrient acquisition. Variations in root development have been associated with differences in water transport efficiency, as the spatial configuration and density of roots and hyphae influence the continuity and conductance of the soil-plant water pathway (Peterson et al. 1993; Steudle et al. 1993).

AM fungi also influence the characteristics of root hairs. Baylis (1975) and St. John (1980) observed that AM fungal-colonized plants often developed thick roots with fewer root hairs, consistent with their reliance on fungal hyphae to

Table 1 Comparison of root morphological responses induced by arbuscular mycorrhizal (AM) and ectomycorrhizal (EcM) symbioses under drought conditions

Parameter	AMF	EcM
Lateral root formation	↑ (Gutjahr and Paszkowski 2013; Yao et al. 2009)	↑↑ (stronger, via signals/volatiles) (Barker et al. 1998; Felten et al. 2009; Ditengou et al. 2015)
Fine root branching	↓ (in highly mycotrophic plants) (Hetrick 1991)	— / variable due to replacement by fungal structures (Baylis 1975; Maherali et al. 2016)
Root diameter	↑ (Baylis 1975; Ma et al. 2018)	↑↑ (due to mantle) (Baylis 1975; Bergmann et al. 2020)
Root hair density	↓ or ↕ (plastic) (Orfanoudakis et al. 2010; Wu et al. 2016)	↓ relevance (replaced by mantle) (St. John 1980; Maherali et al. 2016)
Soil exploration by fungal hyphae	↑↑ (Smith and Read 1997)	↑↑↑ (rhizomorphs/long-distance) (Agerer 2001; Read 1991)

AM fungi generally induce moderate changes in root architecture, whereas EcM elicit stronger structural modifications and a greater fungal contribution to soil exploration. Arrows indicate the direction and relative intensity of the response: ↑ increase, ↑↑ strong increase, ↑↑↑ very strong increase, ↓ decrease, ↕ variable response, and — no consistent effect reported

extend the water absorption surface beyond the rhizosphere. This observation has been corroborated by studies reporting reduced root hair density and length in AM fungal-colonized plants (Orfanoudakis et al. 2010; Sun and Tang 2013). However, this pattern is not always the reality. For example, Wu et al. (2016) found that trifoliate orange seedlings colonized by AM fungi exhibited a significantly higher density of root hairs (185–457% increase in first-order lateral roots) than non-colonized controls, although the length of the root hair was shorter. Under water-deficit conditions, such responses could maximize contact with water films in soil micropores, thus highlighting that AM fungal-induced changes in root hairs can be plastic and adaptive depending on the environmental context. Recent studies further demonstrated that the contribution of root hairs to water uptake is strongly influenced by root–soil contact and soil moisture conditions, particularly under drought stress conditions (Duddek et al. 2023).

Trait-based and evolutionary studies further link AM fungal colonization to characteristic evolutionarily conserved root trait patterns that influence water uptake capacity. Baylis (1975) and St. John (1980) described an evolution towards thick, coarse, sparsely hairy roots. This has been confirmed by large-scale trait analyses showing that plants associated with AM fungi tend to have larger diameter roots and a shorter specific root length (Ma et al. 2018; Bergmann et al. 2020). Maherali et al. (2016) showed that the persistence or loss of AM symbioses across evolutionary lineages is linked to changes in these root traits, highlighting the long-term adaptation of root structure and mycorrhizal water acquisition strategies.

EcM fungi also induce significant changes in root morphology, which promote water uptake under certain conditions. For example, a strong stimulation of lateral root formation has been observed in tree species colonized by EcM fungi (Barker et al. 1998), thereby increasing the number of entry points for fungal hyphae and potentially improving radial water conductance (i.e. water movement from the soil through root tissues to the xylem). Felten et al. (2009) showed that the interaction with *Laccaria bicolor* stimulated lateral root formation in poplar and is associated with auxin accumulation at root tips. Ditengou et al. (2015) identified fungal sesquiterpenes as the signaling molecules responsible for this effect, demonstrating that volatiles compounds emitted by *L. bicolor* reprogram root architecture even before physical contact, promoting an absorptive morphology that enhances fungal access to host carbon and improves root surface area for water uptake.

In addition, EcM fungi form a fungal mantle and Hartig net, structures that increase root diameter and reduce elongation, thus functionally replacing the role of fine absorptive roots (Baylis 1975; St. John 1980; Ma et al. 2018; Bergmann et al. 2020; Maherali et al. 2016). This specialized root morphology aligns with the root traits observed in EcM plants, where investment in thick, densely colonized short lateral roots enhances symbiotic water and nutrient exchange. These architectural modifications, combined with the presence of extraradical mycelium and rhizomorphs, improve access to soil water and the continuity of flow to the root xylem.

Soil aggregation and stability

Soil aggregate stability is a crucial property of soil that affects the movement and storage of water (Fig. 3c) (Amézketa 1999) and determines the adsorption and redistribution of nutrients (Linquist et al. 1997). Fungal hyphae can physically entangle soil micro-aggregates and contribute to their stabilization through the production of extracellular compounds, thereby promoting the formation of macro-aggregates (Tisdall 1994; Graf and Frei 2013). Under drying conditions, AM fungal hyphae may also act as hydraulic bridges connecting water-filled pores to root surfaces, thereby partially maintaining hydraulic continuity across disconnected soil microsites (Miller and Jastrow 2000; Püschel et al. 2020). AM fungi are also associated with the production of compounds collectively referred to as "glomalin" or glomalin-related soil proteins (GRSP), which have long been linked to improved soil aggregation and water retention (Wright and Upadhyaya 1996; Rillig 2004; Janos et al. 2008). However, GRSP is currently regarded as an operationally defined soil fraction extracted through high-temperature citrate extraction procedures rather than a single well-characterized fungal protein (Irving et al. 2021). These extracts may contain heterogeneous compounds, including proteins, humic substances, lipids, carbohydrates, and other soil organic materials co-extracted during the extraction process (Gillespie et al. 2011; Irving et al. 2021). These compounds are released into the soil following hyphal turnover, where they may coat organic matter and mineral particles, contributing to aggregate stabilization and soil structural development (Rillig et al. 2003; Gomathy et al. 2018). However, the molecular identity of glomalin remains under debate. Recent evidence indicates that the antigen recognized by the monoclonal antibody MAb32B11 is likely not a protein but a complex polysaccharide of AM fungal origin, leading to the proposed term "glomalose" instead of glomalin (Alptekin et al. 2025). Protease treatments did not affect the ELISA signal associated with glomalin extracts, whereas periodate treatments targeting polysaccharides significantly

reduced antibody recognition, supporting the hypothesis that the MAb32B11 epitope is carbohydrate-based rather than proteinaceous (Alptekin et al. 2025).

Despite these uncertainties, GRSP and AM-associated extracellular compounds have repeatedly been associated with improved soil aggregation, soil structural stability, and water retention in both field and pot experiments (Wright et al. 1996, 2007; Bedini et al. 2007, 2009; Wang et al. 2015; Gao et al. 2019). Accordingly, their effects on soil water dynamics are currently interpreted mainly through their contribution to aggregate stabilization and pore structure rather than through a direct or uniform increase in soil water repellence (Knorr et al. 2003; Lutgen et al. 2003; Steinberg and Rillig 2003; Feeney et al. 2004; Alptekin et al. 2025). Increasing evidence indicates that AM fungi can alter soil hydraulic properties, including water retention and unsaturated hydraulic conductivity, thereby delaying the onset of transpiration limitation during soil drying (Bitterlich et al. 2018; Abdalla et al. 2023). Because AM fungi can modify soil hydraulic properties, equal soil water contents do not necessarily correspond to equal hydraulic stress in experimentally compared mycorrhizal and non-mycorrhizal systems (Bitterlich et al. 2018; Abdalla et al. 2023).Cheng et al. (2021) further suggested that AM-associated glomalin-related compounds contribute to the formation of water-stable macroaggregates in the mycorrhizosphere, particularly within the 2–4 mm and 0.5–1 mm size fractions.

Some evidence also suggests that EcM fungi can be as important as AM fungi in improving soil structure. Zheng et al. (2014) showed that EcM associations significantly increased water-stable soil aggregation under *Pinus sylvestris*. The most pronounced effect was observed for particles of 2–4 mm. With eight of the nine EcM fungal species used, a significant increase in particle size, from 3 to 14%, was observed compared to the control.

EcM fungi produce small proteins called hydrophobins, involved in various functions, from adhesion of the mycelium to the soil particles surface to the formation of fruiting bodies (Wessels 2000; Wösten and de Vocht 2000). It is thought that these compounds have an additional function, which is to influence the interaction between soil surfaces and water, and the resistance of soil to water infiltration (Rillig 2005; Hallett et al. 2009), due to their amphiphilic nature, which allows for spontaneous formation of a film at the air-water interface. Hydrophobin coatings can alter surface polarity through self-assembly, potentially rendering originally hydrophilic surfaces water-repellent under certain moisture conditions, while conformational changes associated with drying and rewetting may also reduce or reverse this effect (Rillig 2005).

Nutrient uptake by hyphae

During periods of drought, nutrient mobility in the soil decreases sharply because the movement of water (i.e., mass flow) that normally transports nutrients to the root surface is greatly reduced, especially for nitrogen (nitrate and ammonium) (Plett et al. 2020; González-Dugo et al. 2010). In this context, plants colonized by AM or EcM fungi generally maintain better nutrient uptake under drought conditions, as fungal hyphae explore soil volumes inaccessible to roots and ensure ion uptake despite reduced water availability (Augé 2001).

AM fungi are particularly important for phosphorus (P) uptake under periods of drought, as P has low mobility in soils even under optimal soil moisture conditions and becomes even less available when diffusion slows down under water deficit conditions (Hodge et al. 2010). P is absorbed as orthophosphate by high-affinity phosphate transporters in the extraradical hyphae (Harrison and van Buuren 1995), converted into polyphosphate for transport within the fungal hyphae, and subsequently hydrolyzed before transfer to the host plant (Harrison 1999; Bago et al. 2002; Ohtomo and Saito 2005). Moreover, Rausch et al. (2001) identified in *Solanum tuberosum* a subgroup of phosphate transporters belonging to the Pht1 family, a plant family of high-affinity plasma-membrane inorganic P transporters responsible for phosphate uptake under low-P conditions. Within this family, they described a specific subfamily that is expressed exclusively in AM-colonized roots, indicating that these transporters are specialized for receiving phosphate delivered through the mycorrhizal pathway. Although nitrate (NO_3^-) and ammonium (NH_4^+) are generally more mobile in soil, drought reduces their movement toward roots. AM fungi can partially compensate, as shown by Pérez-Tienda et al. (2012), who demonstrated that NH_4^+ transporters in AM fungi have a five-fold higher affinity for NH_4^+ than roots. In addition, recent studies suggest that AM fungal hyphosphere microbial communities can contribute to organic P mineralization through enhanced phosphatase activity and associated bacterial interactions (Wang et al. 2023a, b).

EcM fungi also improve nutrient acquisition during periods of drought, playing a particularly important role in the N cycle. In many forest ecosystems, particularly boreal forests, N becomes the main limiting factor for growth, as it is mostly present in organic forms whose mineralization is slow under dry conditions (Read 1991; Bruns et al. 2002; Read et al. 2004; Toljander et al. 2006; Lin et al. 2017). EcM fungi can access organic N pools by decomposing complex substrates in litter and soil organic matter (Read 1991; Lindahl et al. 2007; Bödeker et al. 2014; Lindahl and Tunlid 2015; Shah et al. 2016). Regarding P uptake during

periods of drought, EcM fungal hyphae can extend farther into the soil than AM fungal hyphae, with mycelial strands capable of transporting P over several meters (Finlay and Read 1986), thus maintaining P supply despite reduced diffusion. EcM hyphae may also access nutrient pools physically unavailable to roots by penetrating mineral microsites and enhancing mineral dissolution processes (Landeweert et al. 2001). Recent evidence further indicates that EcM hyphae can alleviate P limitation by promoting organic P mineralization and the solubilization of mineral-bound P through microbial and biochemical processes in the hyphosphere (Zhang et al. 2023a, b). In addition, EcM fungi can actively weather minerals and mobilize nutrients such as P, K, Mg, and Ca from mineral substrates and bedrock through the exudation of low-molecular-weight organic acids, particularly oxalate, proton release, and direct hyphal–mineral interactions (Landeweert et al. 2001; van Schöll et al. 2008). However, the dense fungal sheath surrounding the roots in EcM fungal associations can act as an apoplastic barrier, limiting the direct entry of nutrients into host tissues, whereas AM fungi do not structurally alter the root surface (Fig. 3c) (Behrmann and Heyser 1992; Bücking et al. 2002).

Regulation of plant aquaporins

AQPs are major intrinsic proteins (MIPs) that form water channels and have a water permeation capacity 10–100 times greater than that of diffusion (Agre et al. 2002). In plant roots, they regulate water permeability across cortical and endodermal cells, where the Casparian strip blocks apoplastic flow and directs water through symplastic and transmembrane pathways, whose permeability is modulated by variations in water availability (Xu and Zwiazek 2020). In fungi, AQPs regulate water flow across hyphal membranes and are increasingly recognized as important determinants of fungal hydraulic properties (Dietz et al. 2011). In mycorrhizal associations, fungal AQPs are positioned to modulate water flow at the plant–fungus interface, complementing root AQPs by providing a parallel pathway for the movement of water from the soil to the root tissues (Maurel and Plassard 2011). Their expression is influenced by symbiotic status and environmental signals, indicating that fungal AQPs dynamically adjust hyphal water permeability according to physiological needs and external water availability (Fig. 3c) (Maurel and Plassard 2011).

In AM symbioses, an early characterization of a plant AQP regulated by AM fungi was reported by Krajinski et al. (2000). These authors found that MtAQP1 transcript levels were significantly higher in AM-colonized *Medicago truncatula* roots than in non-mycorrhizal controls, and functional assays in *Xenopus* oocytes confirmed that this protein facilitates water transport, suggesting that the induction of MtAQP1 by AM fungi may enhance root water permeability. However, most of the research conducted so far has focused primarily on the regulation of plant AQP by AM fungi rather than on the fungal complement itself. Only a few AM fungal AQP have been identified so far. The first AM fungal AQP (i.e., GintAQP1) was identified in *Glomus intraradices* and showed a compensatory expression profile relative to host root AQPs. This AQP has been suggested as a mediator of water redistribution between mycelial and root compartments subjected to water stress (Aroca et al. 2009). Two other AQPs (i.e., GintAQPF1 and GintAQPF2), were subsequently found being strongly induced by PEG-simulated drought (i.e., polyethylene glycol-induced osmotic stress) and contributing to plant drought tolerance, providing direct evidence that AM fungal AQPs can participate in improving host water relations in water deficit situations (Li et al. 2013). To improve root hydraulic conductivity, leaf water potential, and reduce leaf transpiration rate, AM fungi can also up-regulate or down-regulate plant AQP genes in the leaves or roots (Ruiz-Lozano et al. 2006, 2009; Aroca et al. 2008). The roles of AQPs have been established through gene overexpression or silencing (Yu et al. 2005; Peng et al. 2007; Sade et al. 2009). In maize plants, Bárzana et al. (2015) reported that, out of the 36 AQP genes, 16 were differentially regulated by AM symbiosis. Crucially, their results showed that AQP expression patterns were not uniform but varied with drought intensity and duration, with some isoforms upregulated under short-term stress while under prolonged drought conditions their expression was reduced or no longer affected by mycorrhization. Several of these AQPs are capable of transporting water and other solutes of physiological importance, and overall changes in AQP expression correlated with improved performance of AM plants under drought conditions. More recent evidence further supports this differential regulation, with AM fungi inducing specific AQP genes linked to improved drought tolerance, such as *ZmTIP2;3* in maize (Wang et al. 2024) and *LjNIP1;5* in *Lotus japonicus* (Zou et al. 2024), reinforcing the idea that AM symbiosis differentially regulates plant water transport rather than promoting a uniform increase in aquaporin expression.

In EcM fungal associations, the involvement of fungal AQPs in water transport by roots has been demonstrated more clearly. For example, Xu et al. (2016) showed that *Picea glauca* seedlings colonized by *Laccaria bicolor* strains transformed to overexpress a fungal water-transporting AQP exhibited a significant increase in root hydraulic conductance. Two of the top three most frequently expressed genes in EcM fungi are AQP-coding genes (Nehls and Dietz 2014), and strong upregulation of fungal AQPs appears to be characteristic of symbiosis with *Cenococcum geophilum* (Navarro-Ródenas et al. 2013; Xu et al. 2016). In symbiosis

with the desert truffle, it has also been shown that fungal AQPs respond dynamically to drought conditions, suggesting that EcM fungi adjust the abundance of water channels to maintain water flow in drying soils (Navarro-Ródenas et al. 2013). Transcript profiling further revealed a striking upregulation of membrane transporters, including plant AQP genes, sugar transporters, and mycorrhiza-induced small-secreted proteins (Peter et al. 2016), and EcM interaction increased the expression of several transmembrane channels, indicating enhanced substrate exchange between partners (Martin et al. 2010; Peter et al. 2016). Based on physiological and genomic data, Xu and Zwiazek (2020) proposed that the coordinated regulation of fungal and plant AQPs in EcM-colonized roots could adjust root hydraulic conductivity in the event of drought. When water moves across hyphal membranes from the apoplastic to the symplastic space or vice versa, a variety of fungal MIPs regulate this flow (Pettersson et al. 2005; Maurel and Plassard 2011). However, direct demonstrations that EcM-regulated AQP in plants improve drought tolerance remain scarce. Most evidence still relies on gene expression or hydraulic measurements under water deficit conditions. Therefore, further investigations are needed into the function of fungal AQPs and their interactions with root AQPs under drought conditions.

Oxidative stress

Numerous studies have shown that mycorrhiza have beneficial effects on morphological and physiological factors related to plant tolerance to water deficit and salt stress, both of which trigger oxidative stress through reactive oxygen species (ROS) overproduction (Fig. 3d) (Soriano-Martín et al. 2006; Porras-Soriano et al. 2009; Fouad et al. 2014). Specifically, when soil water levels change from well-watered to dry conditions, several mechanisms are activated in plants. For instance, stomatal closure restricts CO_2 fixation and decreases $NADP^+$ production in cells (Wilkinson and Davies 2002; Satoh and Murata 2012). Consequently, oxygen acts as an electron donor, producing the superoxide radical (O_2^-) (Cadenas 1989), which the Haber–Weiss reaction can combine with hydrogen peroxide (H_2O_2) to create the hydroxyl radical ($OH\cdot$) (Sairam et al. 1998). As a side effect, this severe oxidative stress can result in lipid peroxidation, membrane damage, and eventually cell mortality (Apel and Hirt 2004).

ROS play a central and tightly regulated dual role in AM symbiosis: functioning as signaling molecules during symbiosis development and as potential sources of oxidative stress. Interestingly, H_2O_2 accumulation in cortical cells containing arbuscules suggests oxidative stress is even involved in arbuscule degradation during their life cycle (Wu et al. 2014). To counteract drought-induced ROS, AM fungi possess their own intrinsic antioxidant systems (Lanfranco et al. 2005; González-Guerrero et al. 2010) and enhance the host's enzymatic defenses, including superoxide dismutase (SOD), catalase (CAT), and ascorbate peroxidase (APX), as well as non-enzymatic defenses (e.g., ascorbate, carotenoids, glutathione) (Wu and Zou 2017). This coordinated regulation links redox homeostasis with molecular drought-response pathways, such as the activation of the mitogen-activated protein kinase (MAPK) cascade observed in *Eucalyptus grandis* (Wang et al. 2023a, b).

Meta-analyses confirm that AM fungal inoculation increases plant antioxidant enzyme activity by approximately 16% (Lokhandwala and Hoeksema 2019) and significantly reduces membrane damage across diverse species (Chandrasekaran 2022). Experimental studies highlight this versatility under severe drought; AM fungi stimulate SOD and peroxidase in chicory (Langeroodi et al. 2020), boost soluble sugars in sesame (Gholinezhad et al. 2020), and promote the accumulation of protective phenolic compounds, carotenoids, and anthocyanins in crops like wheat, maize, and lettuce (Baslam and Goicoechea 2012; Begum et al. 2019; Bitaraf et al. 2020).

Compared to AM fungi, EcM-mediated antioxidant responses during drought are less understood and appear highly context-dependent. Studies on *Nothofagus dombeyi* associated with *Descolea antartica* and *Pisolithus tinctorius* showed a significant increase in antioxidant enzymes (SOD, CAT, APX) to eliminate ROS (Alvarez et al. 2009). Recent transcriptomic approaches suggest that both plant and EcM fungal partners actively contribute to these defenses under stress (Li et al. 2022; Zhang et al. 2023a, b). Nevertheless, direct separation of fungal and plant antioxidant activities in symbiotic roots remains challenging (Mateus et al. 2024), and responses can vary greatly depending on the specific combination of fungal and plant species or the nature of the environmental stressor (Langenfeld-Heyser et al. 2007).

Mycorrhizal application for mitigation of drought impact

Mycorrhizal fungi show strong potential for mitigating the adverse effects of drought in agricultural and forest ecosystems. Recent studies highlight the value of AM fungi as a nature-based solution for maintaining plant productivity and multiple soil functions in the face of increasingly frequent droughts (Tang et al. 2024). However, large scale implementation of these benefits remains challenging and requires concerted progress in fungal and plant selection, breeding strategies and soil environment management.

Selection of optimal fungal–plant partnerships and the role of mycorrhizal diversity

Not all mycorrhizal strains or plant genotypes provide equivalent advantages under drought, and experimental evidence indicates that specific combinations of fungal and host genotypes can strongly influence the costs and benefits of the symbiosis (Johnson et al. 2015; Rog et al. 2025). Experimental work has shown that AM fungi communities originating from drier or harsher environments, as well as particular isolates of *Rhizophagus*, *Claroideoglomus* and *Funneliformis*, can confer superior drought tolerance by enhancing water and nutrient uptake and regulating stress physiology (Benhiba et al. 2015; Mirshad and Puthur 2016; Zhang et al. 2018). For example, Querejeta et al. (2006) showed that native drought-adapted AM fungi improved plant water status, stomatal conductance, nutrient uptake, and long-term growth more effectively than nonnative AM fungi under semiarid field conditions. Similarly, AM fungal communities in grasslands and cropping systems respond strongly to water availability, with drought selecting specific functional groups and altering community composition (Emery et al. 2022; Albracht et al. 2023).

For EcM systems, recent work shows that specific taxa such as *Clitocybe nuda* and *Cortinarius distans* are particularly effective at seedling mycorrhization and can improve conifer establishment, while the absence of suitable EcM colonization can limit tree establishment in open or degraded sites (Policelli et al. 2020; Assad et al. 2022).

Together, these studies support the idea that targeted selection of fungal–plant partnerships can be beneficial under specific environmental conditions.

However, in long-lived systems such as forests, where environmental conditions vary over time and drought regimes are increasingly unpredictable, reliance on single "optimal" fungal–plant pairs may represent a risky strategy. Increasing evidence suggests that drought resilience may instead emerge from functionally diverse mycorrhizal communities, in which complementary and partially redundant fungal traits buffer host performance under variable water availability. In both agricultural and forest ecosystems, multi-species AM fungi assemblages and diverse EcM communities have been shown to enhance the stability of plant performance under drought by maintaining resource acquisition and stress tolerance across fluctuating conditions (Querejeta et al. 2006; Köhler et al. 2018; Bakker et al. 2019; Albracht et al. 2023). In forest trees, drought tolerance may also depend on specific associations between host plants and mycorrhizal fungal communities. For example, Gehring et al. (2017) demonstrated that drought-tolerant genotypes of *Pinus edulis* were consistently associated with distinct EcM fungal communities that enhanced seedling growth and survival under drought conditions. These findings indicate that, particularly for forest trees, maintaining a broad diversity of compatible host genotypes and mycorrhizal fungi may provide greater long-term flexibility and resilience than narrowly optimized fungal–plant combinations.

Breeding for mycorrhiza-responsive crops and trees

Conventional breeding methods have rarely targeted mycorrhizal responsiveness, even though cultivated varieties and tree provenances differ considerably in their dependence on AM and EcM fungal symbioses (Karst et al. 2009; Baum et al. 2015; Ryan and Graham 2018; Kujawska et al. 2023). A forward-looking strategy involves selecting plants capable of specifically recruiting and more effectively utilizing mycorrhizal communities in water deficit situations. Despite clear evidence that tree species and provenances vary widely in their dependency on and responsiveness to mycorrhizal fungi, conventional breeding programs have seldom incorporated belowground symbiotic traits into selection criteria. Instead, they have focused primarily on aboveground performance and timber production, thereby overlooking a major driver of forest resilience and ecosystem services (Bakker et al. 2019). In parallel, experimental work shows that plant genotypes differ in their ability to maintain mycorrhizal colonization and water-deficit tolerance, suggesting that mycorrhizal dependency and symbiotic efficiency could be incorporated as selection criteria in breeding programs for agricultural crops and forest trees (Fernández-Lizarazo and Moreno-Fonseca 2016; Gehring et al. 2017; Bowles et al. 2018; Manzanedo et al. 2018). In the long term, integrating plant–mycorrhizal interactions into breeding programs could make it possible to produce varieties that intrinsically rely on AM or EcM fungi to maintain hydraulic conductance, nutrient acquisition and yield stability under drought conditions.

In forest ecosystems, opportunities to enhance drought resilience through conventional breeding approaches may be constrained by the long generation times and complex ecological interactions that characterize forest systems. In this context, enhancing mycorrhizal-mediated drought resilience may rely less on breeding per se and more on promoting the natural regeneration of tree species associated with effective EcM fungal communities, as well as on maintaining tree species diversity to support a functionally diverse and resilient fungal pool (Grove et al. 2019; Southam et al. 2022; Sachsenmaier et al. 2024). In addition, drought-induced tree mortality can alter EcM fungal community composition and potentially constrain seedling establishment and ecosystem recovery by reducing the abundance of beneficial fungal partners (Mueller et al. 2019).

Innovation in agricultural and forestry practices

Mycorrhizal applications cannot succeed if the surrounding soil environment is hostile to fungal survival or function. In agricultural systems, practices such as intensive tillage, high mineral fertilization and low organic matter inputs can strongly reduce mycorrhizal colonization and suppress the benefits of inoculation (Avio et al. 2013; Bowles et al. 2016; Zinati et al. 2025). Mechanical soil disturbance can disrupt AM fungal hyphal networks, reduce propagule abundance, and alter AM fungal community composition, thereby limiting fungal persistence and functioning in soils (Schnoor et al. 2011). In addition, excessive N and P fertilization can suppress mutualistic fungi while favoring pathogenic fungal guilds, partly through nutrient-induced shifts in plant community composition and reduced plant carbon allocation to AM fungi (Lekberg et al. 2021). In contrast, reduced tillage, maintenance of soil organic carbon, moderate nutrient inputs and diversified crop rotations tend to support more diverse and functionally robust AM fungal communities, which in turn can improve plant water use and drought tolerance (Bowles et al. 2016; Boutasknit et al. 2021; Kozjek et al. 2021; Thapa and Mowrer 2022; Li et al. 2025).

In forest ecosystems, management practices influence mycorrhizal functioning not only through tree species composition, but also through soil disturbance associated with plantation establishment and harvesting operations. Intensive site preparation and soil compaction caused by heavy machinery can disrupt EcM mycelial networks, reduce fungal diversity, and impair seedling colonization and establishment (Lazaruk et al. 2008; Kranabetter et al. 2017). Similarly, clear-cutting and the removal of living host roots can sharply reduce EcM inoculum potential, with regenerating seedlings showing lower colonization when distant from residual trees (Teste and Simard 2008; Bingham and Simard 2012). Wildfires, particularly high-severity events, can further profoundly alter forest soil fungal communities by drastically reducing EcM fungi, disrupting root-associated fungal networks, and promoting stress-tolerant pyrophilous and pathogenic taxa (Philpott et al. 2025).

Recent evidence from a tree-diversity experiment indicates that communities combining AM- and EcM-associated species outperformed monocultures during the 2018–2020 European drought, highlighting the importance of mixed mycorrhizal strategies for forest resilience (Sachsenmaier et al. 2024).

Beyond species composition, silvicultural approaches that limit soil disturbance and retain biological legacies, such as living trees, intact forest-floor patches, and coarse woody debris (i.e., variable tree retention), have been shown to preserve EcM fungal inoculum sources and facilitate rapid recolonization of regenerating seedlings (Hewitt et al. 2018; Simard 2021). Aggregated retention, in particular, can maintain EcM fungal community composition closer to that of unharvested forests than dispersed retention or clear-cut systems (Hewitt et al. 2018). Large-scale forest surveys and meta-analyses further indicate that mixed-mycorrhizal strategies and reduced structural homogenization enhance forest productivity which likely underpins increased drought resilience (Luo et al. 2023; Jia et al. 2025).

Overall, these findings suggest that successful drought mitigation through mycorrhizal utilization depends not only on selecting appropriate fungal partners or tree species, but also on adopting agricultural and forestry practices that minimize soil disturbance and sustain diverse, well-connected mycorrhizal networks at the field and stand scale.

Broadening the target beyond AM fungi

Research on mycorrhizal contributions to drought mitigation has so far focused predominantly on AM fungi, largely reflecting the emphasis on agricultural and grassland systems, even though EcM fungi dominate root symbioses of most woody species in temperate and boreal forests and play a central role in carbon and nutrient cycling (Smith and Read 2008; van der Heijden and Horton 2009; Hawkins et al. 2023). Although most research on mycorrhizal drought mitigation has focused on AM fungi, evidence indicates that EcM fungi can also influence plant water relations by enhancing soil exploration and facilitating access to spatially heterogeneous water sources, including through ERM and CMN (Egerton-Warburton et al. 2007; Simard 2009; Querejeta et al. 2012; Policelli et al. 2020). However, mechanistic studies of EcM fungal contributions to drought resilience remain scarce compared with those on AM fungi, particularly with respect to strain-specific effects on water transport, root architecture, and hormonal regulation. Broadening drought-mitigation strategies beyond AM fungi to include functionally characterized EcM taxa and mixed AM–EcM assemblages is therefore especially relevant for forest and agroforestry systems dominated by woody hosts.

Conclusions

Despite notable differences in morphology and root colonization patterns, both AM and EcM fungi influence plant drought responses through multiple interacting mechanisms affecting soil–plant water relations, hydraulic functioning, and plant physiological regulation. While early studies mainly emphasized enhanced water uptake as the principal role of mycorrhizal fungi under drought, recent research highlights the importance of additional mechanisms involving soil hydraulic properties, root–soil interface conductance, fungal network architecture, and regulation of plant water transport pathways.

However, the precise hydraulic contribution of mycorrhizal fungi remains insufficiently quantified, particularly regarding the direct transfer of water from fungal hyphae to host plants and the relative importance of fungal traits involved in water transport. Increasing evidence suggests that many mycorrhizal effects on drought responses may arise indirectly through modifications of soil structure, hydraulic continuity, and root–soil interactions rather than exclusively through direct hyphal water transport. Further research is needed to better understand the role of fungal AQPs and their interaction with plant AQPs, as well as the regulation of water transport pathways at the symbiotic interface.

Overall, this review highlights both the similarities and the functional differences between AM and EcM symbioses in the context of drought stress. AM-mediated drought responses likely emerge from multiple interacting mechanisms involving soil hydraulic properties, root–soil interface conductance, fungal network architecture, and plant physiological regulation, whose relative importance remains highly context dependent. Future research integrating soil physics, fungal functional traits, and plant hydraulics will be essential to better predict mycorrhizal contributions to plant drought responses under changing climatic conditions.

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