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Mycorrhizal Symbioses: Mechanisms, Ecological Function and Responses to Global Change

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Abstract

Most land plants acquire mineral nutrients through fungal partners rather than through roots alone. This review examines the cellular basis of that partnership, the differences between the principal mycorrhizal types, and the consequences for plant communities and soil processes. Fossil evidence places arbuscular associations in the earliest land floras, and roughly seventy percent of vascular plant species retain them today. Recognition begins with a reciprocal exchange of diffusible signals, proceeds through a conserved symbiosis signalling pathway shared with nitrogen-fixing associations, and ends in a highly branched fungal structure enclosed by a plant-derived membrane across which phosphate moves inward and carbon moves outward. Work with isotope tracers has shown that the fungus receives both sugars and fatty acids, which it cannot make for itself, and that plants preferentially reward the more productive fungal partners. At the ecosystem scale the type of association predicts how nitrogen is cycled, how much carbon accumulates in soil, and how strongly plant growth responds to rising carbon dioxide. Responses to warming, nitrogen deposition and land conversion differ between types, so shifts in the composition of these associations are likely to alter nutrient cycling in ways that current models capture only in outline.

Keywords: Arbuscular Mycorrhizam Ectomycorrhiza, Symbiosis Signalling, Phosphate Uptake, Soil Carbon.

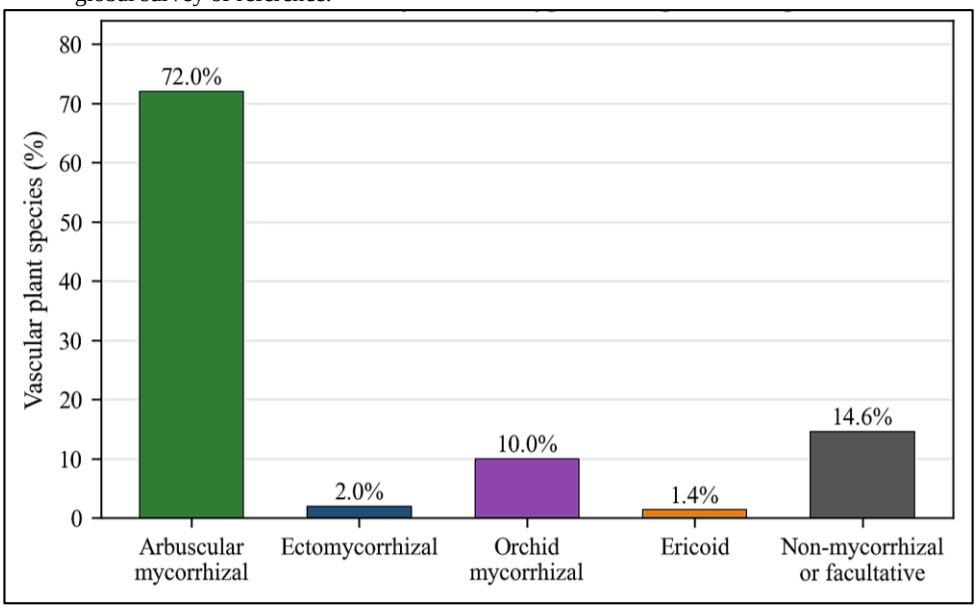
1. INTRODUCTION

The root systems of most terrestrial plants are not, functionally speaking, the organ that absorbs mineral nutrients. That role belongs largely to fungal hyphae that colonise the root and extend into soil pores far too narrow for a root hair to enter. The association is ancient. Fungal structures indistinguishable from modern arbuscules occur in the Rhynie chert, dated to roughly 400 million years, in plants that had no true roots at all .[1] This has led to the view that the symbiosis was a precondition for the colonisation of land rather than a later refinement of it .[2]

The association remains close to universal. Surveys of the vascular flora indicate that around seventy percent of species form arbuscular mycorrhizas, roughly two percent form ectomycorrhizas, and smaller fractions form the specialised orchid and ericoid associations, with the remainder either non-mycorrhizal or inconsistently colonised .[3] Figure 1 shows this distribution. The numerical dominance of the arbuscular type conceals the disproportionate importance of ectomycorrhizal plants, which include most trees of boreal and temperate forests and therefore govern nutrient cycling over large areas of the land surface.

This paper reviews the mechanisms by which these associations operate and the ecological consequences that follow from them. The first sections deal with the diversity of association types and the molecular events that establish them. Later sections consider what the association does at the scale of communities and ecosystems, how it responds to environmental change, and where attempts to use it in agriculture have succeeded or failed.

Fig 1: Approximate share of vascular plant species forming each mycorrhizal type, based on the global survey of reference. [3]



2. THE PRINCIPAL TYPES OF ASSOCIATION

Four associations are usually distinguished, and they differ in fungal partner, in the anatomy of the interface and in the nutrients they deliver. Table 1 summarises the comparison. The arbuscular symbiosis involves fungi of the subphylum Glomeromycotina, which are obligate biotrophs unable to complete their life cycle without a host. Hyphae penetrate the cortical cell wall but not the plasma membrane, and branch into the tree-like arbuscule that gives the type its name. The ectomycorrhizal association evolved repeatedly in the Basidiomycota and Ascomycota, and its hyphae remain between cells, forming a sheath around the root tip and a network in the apoplast .[4]

The functional distinction that matters most is the ability to attack organic material. Arbuscular fungi possess a limited repertoire of degradative enzymes and take up mineral nutrients, principally phosphate, from the soil solution. Many ectomycorrhizal and ericoid fungi retain enzymes inherited from saprotrophic ancestors and can mobilise nitrogen and phosphorus bound in organic matter .[5] This difference underlies much of the ecological contrast discussed later in this paper, since it determines whether the symbiosis competes with free-living decomposers or merely harvests what they release.

Identifying the fungal partners has depended almost entirely on molecular methods, because many taxa sporulate rarely and their mycelium carries few distinguishing characters. Sequencing of ribosomal markers from roots and soil has shown that the number of described arbuscular fungal species is small, in the low hundreds, against the tens of thousands of plant species they serve, so specificity is generally low and one fungal individual may colonise several plant species at once .[3] Ectomycorrhizal fungi are far more numerous and considerably more specific, with lineages restricted to particular host families .[4] The contrast matters for the ecology discussed later, since an arbuscular network can link unrelated plants growing together while an ectomycorrhizal network usually connects members of a single host group.

Table 1. Comparison of the principal mycorrhizal types Compiled from references.[3,4,5]

Type	Fungal lineage	Typical hosts	Interface	Main benefit to plant
Arbuscular	Glomeromycotina	Most herbs, grasses, many tropical trees	Intracellular arbuscular	Phosphate, zinc, water
Ectomycorrhizal	Basidiomycota, Ascomycota	Pinaceae, Fagaceae, Dipterocarpaceae	Sheath and intercellular network	Organic and mineral nitrogen
Ericoid	Ascomycota (Helotiales)	Ericaceae of acid heath and peat soils	Coils in epidermal cells	Nitrogen from recalcitrant organic matter
Orchid	Basidiomycota (Rhizoctonia group)	All Orchidaceae during germination	Intracellular pelotons	Carbon and nutrients to the seedling

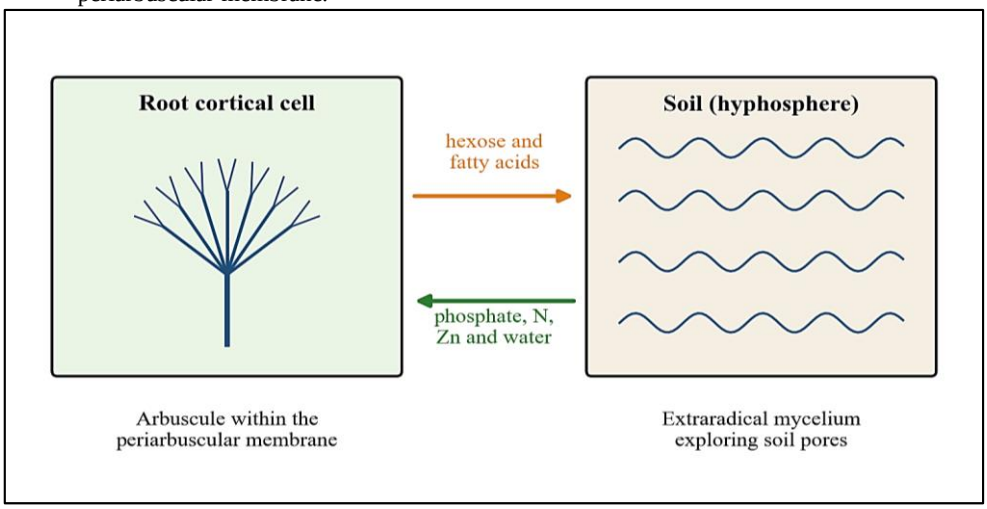
3. ESTABLISHING THE ARBUSCULAR SYMBIOSIS

Colonisation begins before contact. Roots release strigolactones into the rhizosphere, and these stimulate hyphal branching in germinating fungal spores. The fungus replies with lipochitooligosaccharides and short-chain chitin oligomers, collectively termed Myc factors, which the plant perceives through lysin-motif receptor kinases .[6] Signal perception activates a pathway involving nuclear calcium spiking, a calcium and calmodulin-dependent kinase and its transcriptional target, and this same pathway is required for nodulation in legumes. Its conservation indicates that the machinery for accommodating nitrogen-fixing bacteria was recruited from a much older fungal programme .[7]

After contact the host builds a transient structure, the prepenetration apparatus, which guides the hypha through the epidermal cell. In the cortex the hypha branches repeatedly and the plant plasma membrane invaginates around it to form the periarbuscular membrane. This membrane carries a distinct set of transporters, including mycorrhiza-specific phosphate transporters whose loss abolishes the nutritional benefit without preventing colonisation. Figure 2 shows the arrangement schematically. The interface is short lived; individual arbuscules degenerate within days and are replaced, so the exchange surface is continually renewed .[4]

What the fungus receives in return was long assumed to be sugar alone. Two studies published together showed otherwise. Isotope labelling and analysis of mutants demonstrated that the fungal lipids are synthesised by the plant and transferred across the interface, and that a plant fatty-acid biosynthetic pathway is induced specifically in arbuscule-containing cells .[8,9]Since glomeromycotinan genomes lack the genes for cytosolic fatty-acid synthesis, this dependence explains why these fungi cannot be cultured away from a host and why the association has never reverted to a free-living state.

Fig 2: Bidirectional exchange at the arbuscular interface. Carbon moves to the fungus as hexose and as fatty acids, while phosphate and other mineral nutrients move to the plant across the periarbuscular membrane.[8,9]



4. STABILITY OF THE EXCHANGE

An exchange of this kind invites cheating, since a fungus that took carbon without delivering phosphate would gain at the expense of its host. Experiments in which single root systems were offered fungal partners of differing quality showed that plants direct more carbon to the partner supplying more phosphate, and that the fungus reciprocally allocates more phosphate to the more generous host. The reward operates at the level of individual root regions rather than the whole plant, which is what allows discrimination among partners sharing one mycelium .[10]

The benefit is nevertheless conditional. A meta-analysis of inoculation experiments found responses ranging from strong growth promotion to net depression, with the outcome depending on soil phosphorus availability, on the identity of both partners and on light availability to the host.[11] Plants growing in phosphorus-rich soil suppress the symbiosis through systemic signalling, which is the expected response when the carbon cost exceeds the nutritional return. The association is therefore best described as occupying a continuum between mutualism and parasitism whose position shifts with conditions.[12]

5. CONSEQUENCES FOR COMMUNITIES AND SOILS

Mycorrhizal fungi influence plant coexistence as well as plant nutrition.[13] In microcosms, increasing the number of arbuscular fungal species increased plant diversity and productivity, because different fungi favoured

different hosts.[14] In the field, soil biota accumulate around established plants and generate feedbacks that may be negative, which promotes turnover, or positive, which promotes dominance. The direction depends on mycorrhizal type: ectomycorrhizal tree seedlings tend to experience positive feedback, whereas arbuscular species more often experience negative feedback mediated by accumulating pathogens, and this difference predicts patterns of recruitment in temperate forests.[15]

The most consequential ecosystem effect concerns carbon and nitrogen. Under the framework proposed by Phillips and colleagues, stands dominated by arbuscular trees cycle nutrients rapidly through inorganic pools, while ectomycorrhizal stands rely on organic nitrogen mobilised by their fungal partners and accumulate litter that decomposes slowly.[16] Because those fungi compete with free-living decomposers for nitrogen, they slow decomposition and increase the quantity of carbon retained in soil; a global synthesis found consistently higher soil carbon under ectomycorrhizal vegetation after accounting for climate and productivity.[17] Fungal hyphae also bind soil particles into aggregates, which protects organic matter physically and improves water relations.[18]

These effects are large enough to appear in global maps. Analyses of forest inventory data covering more than a million plots show that the distribution of tree symbioses follows the climatic controls on decomposition, with ectomycorrhizal dominance where cold or dry conditions slow the release of nutrients from litter and arbuscular dominance where decomposition is rapid.[19] Global maps of mycorrhizal vegetation constructed on this basis link the distribution of symbiosis types to terrestrial carbon stocks.[20]

6. RESPONSES TO ENVIRONMENTAL CHANGE

Rising atmospheric carbon dioxide increases plant growth only where nutrient supply permits, and mycorrhizal type is a strong predictor of which stands respond. A synthesis of free-air enrichment and chamber experiments found that plants with ectomycorrhizal partners showed substantial biomass gains under low nitrogen availability, while arbuscular plants under the same conditions showed little response.[21] The proposed explanation is that ectomycorrhizal fungi can mobilise organic nitrogen and so relieve the constraint, whereas arbuscular fungi cannot.

Nitrogen deposition acts in the opposite direction. Chronic addition reduces colonisation, shifts fungal community composition and lowers the diversity of ectomycorrhizal fungi, effects observed consistently across long-term experiments in temperate forests. Warming shifts the geographic ranges of both partners, and because fungal and plant ranges need not move together, novel combinations are likely. Conversion of land to intensive agriculture reduces arbuscular fungal abundance and diversity through tillage, phosphate fertilisation and the loss of continuous host cover.

The practical response has been to sell fungal inoculants, and here the evidence is uneven. Field trials show benefits that are largest in degraded or phosphorus-poor soils and often negligible in fertilised systems where native fungal communities are already present and plant demand is low.[11] Management that maintains host cover through cover cropping and reduces soil disturbance tends to support the native community more reliably than inoculation does.

Drought interacts with the symbiosis in both directions. Colonised plants often maintain higher water potential during dry spells, since hyphae reach water held in pores that roots cannot enter and improve the contact between soil and root surface. Severe drying nevertheless damages the extraradical mycelium, and repeated cycles of drying and rewetting reduce the length of hyphae in soil. Whether the net effect of a drier climate is protective or damaging therefore depends on the severity of the episodes rather than on annual averages, which is one reason field results have been inconsistent.

7. NETWORKS BETWEEN PLANTS AND THE LIMITS OF THE EVIDENCE

A single fungal mycelium can colonise the roots of several plants, which raises the possibility that resources move between individuals through the fungus. Isotope labelling in a Douglas fir and paper birch system reported a net transfer of carbon between trees of different species, with the direction depending on shading.[22] A later field experiment labelled the canopies of mature spruce trees and detected the label in neighbouring trees of other species, indicating transfer at ecologically meaningful scales in an old forest.[23]

These results have been extended in popular accounts into claims that trees deliberately support their offspring and warn neighbours of attack through a fungal network. A systematic review of the primary literature examined the evidence for three such claims and found it much weaker than the secondary literature suggests: field evidence that networks are widespread in forests is limited, the effect of networks on seedling performance is inconsistent in sign, and no peer-reviewed study has demonstrated defence signalling between adult trees through a network in the field. The review also documented citation practices in which unsupported claims accumulated support through repetition.[24]

The reasonable position is that transfer occurs, that its magnitude relative to a tree's carbon budget is generally small, and that transfer through a shared mycelium is difficult to separate from transfer through soil solution or through decomposing material. Distinguishing these routes requires labelling designs that few studies have implemented. The topic is a useful reminder that a mechanism demonstrated under controlled conditions

does not establish an ecological function, and that the strength of a claim should be judged from the primary measurements rather than from how often it has been repeated.

8. CONCLUSION

Mycorrhizal associations are the normal condition of terrestrial plants, not an accessory to it. The molecular events that establish the arbuscular symbiosis are now traced from the first diffusible signal to the transporters that carry phosphate and lipids across the interface, and the mechanisms that keep the exchange stable are partly understood. At larger scales the type of association predicts how nitrogen is cycled, how much carbon soils retain and how vegetation responds to enrichment of the atmosphere. The main gaps lie between these scales. Fungal community composition is still poorly represented in ecosystem models, the fate of the carbon delivered to fungi is quantified for few systems, and the consequences of reassembling plant and fungal communities under a changing climate remain largely unexamined. Progress on these points would improve predictions of soil carbon storage more than further work on the signalling pathway alone.

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