Front. Agr. Sci. Eng. 2025, 12(1): 37–46 https://doi.org/10.15302/J-FASE-2024578
REVIEW

Networking via mycorrhizae

Xiaofan MA[1,2], Erik LIMPENS (✉)[1]

1 Laboratory of Molecular Biology, Department of Plant Sciences, Wageningen University & Research, Wageningen 6708 PB, the Netherlands.
2 State Key Laboratory of Nutrient Use and Management; College of Resources and Environmental Sciences; Key Laboratory of Plant–Soil Interactions (Ministry of Education), China Agricultural University, Beijing 100193, China.

KEYWORDS

Mycorrhizal fungi, common mycorrhizal network, signal transfer, defensive response

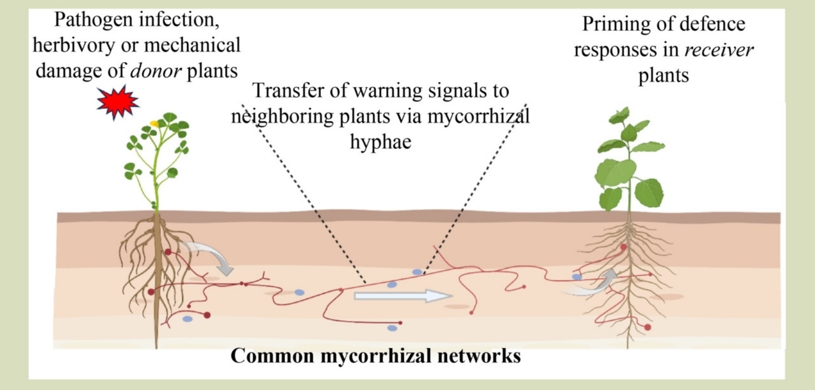
HIGHLIGHTS

- Evidence for interplant communication via common mycorrhizal networks is reviewed.
- Potential transport routes for semiochemicals via fungal hyphae are identified.
- Drivers of signal exchange via CMNs are discussed.

Received May 7, 2024;
Accepted July 15, 2024.

Correspondence: erik.limpens@wur.nl

GRAPHICAL ABSTRACT



ABSTRACT

Interplant communication is of vital importance for plant performance in natural environments. Mycorrhizal fungi have emerged as key contributors to the below ground communication between plants. These mutualistic fungi form connections between the roots of plants via their hyphae, known as common mycorrhizal networks (CMNs). These hyphal networks are thought to be important ways for the exchange of signals between plants. This paper reviews the evidence for CMN-based transfer of semiochemicals between plants upon exposure to pathogen infection, herbivory or mechanical damage. Potential transport routes are explored, asking whether the fungi can actively contribute to the distribution of such signals within the network and discussing potential drivers for signal exchange. It is concluded that identification of the signals that are exchanged remains an important challenge for the future.

1 Introduction

Mycorrhizal fungi colonize the roots of a wide range of land plants, holding extraordinary significance for ecosystem functioning[1]. These mutualistic fungi are broadly categorized as ectomycorrhizae (EcM) and endomycorrhizae, which include ericoid (ErM) and arbuscular mycorrhizae (AM)[2]. Ectomycorrhizal hyphae penetrate in between the cells of the root epidermis and outer cortex to form an apoplastic symbiotic interface for nutrient exchange called the Hartig net[3]. Hyphae of endomycorrhizae are typically hosted inside root cortex cells, where they can form intimate host interfaces, called arbuscules in case of AM fungi[4]. Each category can establish symbiotic relationships with host plants, wherein the plants supply carbon to the fungi in return for essential nutrients, such as nitrogen and phosphorus. The extraradical fungal hyphae that grow out into the soil can efficiently scavenge these nutrients from the soil, where they are often scarcely available for the plant. Additionally, mycorrhizal associations contribute to enhancing plant tolerance to a variety of both biotic and abiotic stresses[5,6].

The development of extraradical hyphae allows the formation of hyphal connections between the roots of two or more host plant species, forming a network known as a common mycorrhizal network (CMN) through which nutrients and signals can be exchanged between plants. This concept has been dubbed the *wood-wide web*[7], in forest settings, although the extent and importance of such fungal interplant connections has recently been critically questioned[8]. Especially, evidence for the role of CMNs in carbon (or mineral) transfer as a nutrient source from plant to plant, except for mycoheterotrophic plants, is often weak, although opinions vary within the research community[9–11]. Due to the tendency of ErM hyphae to concentrate near the host roots and their extraradical mycelia extending only a few millimeters into the surrounding soil, the CMNs formed by ErM fungi likely operate only at a local spatial scale[12]. In contrast, the hyphal lengths of AM and EcM fungi vary significantly, ranging from 10 to 100 m of hyphae per gram of soil[13], and AM hyphae can extent at least several tens of centimeters from the host root, while EcM can form networks extending several meters from the roots. However, the exact length of a CMN in natural systems is very difficult to assess. Also, the potential fusion (anastomosis) of hyphae among genetically related fungal individuals can potentially further extent the connectivity within CMNs[14]. Consequently, AM and EcM fungi have become focal points in discussions about CMNs[13,15].

Various studies have suggested that CMNs can transport H_2O, photosynthetic C, soil N, P, and other mineral nutrients between plants[16–19], although proof of nutrient transfer is often indirect. In recent years, the potential for CMNs to transport larger molecules such as lipids (especially in the form of triacylglycerol), sugars (notably hexoses), and amino acids has been increasingly explored[18,20–23]. The sharing of nutrients by CMNs can positively influence the growth and development of the connected plants. For example, isotope tracing experiments have revealed an intriguing dynamic in the interaction between flax (a C3 plant) and sorghum (a C4 plant) when connected via AM fungi forming a CMN[24]. Despite flax making a modest C investment, it remarkably acquired 80% to 94% of the mineral nutrients supplied by the CMN, which significantly enhanced its growth. In contrast, the neighboring sorghum expended substantial C resources to the CMN with limited reciprocal benefits, but without significant impact on its growth. The overall biomass production in this mixed culture surpassed the mean of the two monocultures[24], indicating that CMNs may be crucial for fostering nutrient use efficiency to boost productivity. A follow up study using *Medicago truncatula* showed that AM fungi can distinguish individual host plants sharing a CMN based on the varying C source strength of different host plants[25]. The fungi allocated more nutrients to the plant that provided most C, in line with previous work from *in-vitro* systems[26]. This was explained by the conceptual framework of a biological market theory, where supply and demand determine the exchange-rate for commodities within the network[27,28]. However, the molecular mechanisms that underlie such a framework remain to be unraveled. A meta-analysis showed that the response of seedlings to CMNs ranges from positive to negative in a roughly equal number of cases[18]. CMNs can also enhance competition between individuals leading to exaggerated growth inequalities between connected plants[29]. Given the fact that mycorrhizal fungi can offer benefits beyond nutrient supply, cost and benefits may be difficult to assess[18,30]. In several recent reviews the role of CMNs in nutrient exchange, the quantification of dynamic nutrient transfer and predictions regarding the drivers of the resource movement have been discussed[31,32].

In this review, we focus on the role of CMNs in the transfer of semiochemicals (or infochemicals), that is, informational molecules released by an organism that affect the behavior of other individuals in the network. In 2001, Chamberlain et al.[33] discovered that aphid-infested beans can release bioactive compounds into the hydroponic medium that conferred increased attractiveness of uninfested plants to parasitoids. Work by Dicke and Dijkman[34] indicated that above ground herbivore attacked plants could send chemical information to neighboring plants via the soil. Therefore, it was postulated that CMNs could potentially be important conduits for signaling molecule communication between connected plants. In recent years, intriguing roles for CMNs in transmitting warning signals between plants have indeed been reported[35–37]. In this review, we discuss the evidence for such CMN-based information transfer, potential signal transmission pathways and explore the controllers of signal delivery.

2 Evidence of CMN-based interplant communication

Song et al.[37] were pioneers in illustrating the supportive role of CMNs in the upregulation of defense genes and putative defensive enzymes in non-invaded neighboring tomato plants (*Lycopersicon esculentum*). Upon establishing a CMN with the AM fungus *Funneliformis mosseae*, tomato plants were inoculated with the pathogen *Alternaria solani* to act as *donor* plants. These donors undergo immune responses with increased activities of presumed defensive enzymes. Six defense-related genes were also activated in adjacent non-infected *receiver* plants that were connected by the CMN, concomitant with an increased activity of defense-related enzymes. To rule out possible effects from root exudates and mycorrhization, pathogen-challenged donor plant and healthy receiver plant were separated by a waterproof membrane. In the absence of a CMN, the expression of defense-related genes was not significantly affected in the receiver plants.

Babikova et al.[38] shifted their focus to the role of CMNs in signal transmission under herbivory. Donor faba bean plants (*Vicia faba*) infested with aphids, emitted methyl salicylate (MeSA), which acted as a repellent to the aphids and an attractant for their natural enemies, parasitic wasps. The non-infested receiver plants, connected by AM fungi to the donor plant in a CMN, started to emit a mixture of volatile organic compound (VOC) mixtures like that released by the donor plants, especially MeSA, while neighboring plants without CMN connections did not effect such a defensive response. To prevent airborne transmission of VOCs, all aboveground portions of the plants were enclosed in plastic bags when aphids were introduced to the donor plants.

Subsequent research, using donor tomato plants infested with the caterpillar *Spodoptera litura*, demonstrated the interplant signaling function of a CMN formed by the AM fungus *Funneliformis mosseae* in inducing defense-related genes and activation of the jasmonate (JA) pathway leading to increased resistance in receiver plants upon herbivory[36]. Similarly, application of MeJA to the donor plants caused an increase in JA concentrations and signaling in the receiver plants. In this study, the use of a JA biosynthesis-deficient mutant, *spr2*, as the donor plant failed to induce defense responses in the connected non-infested plants, leading to unaltered insect resistance in the receiver plants. This suggested that JA signaling was required for the observed CMN-mediated interplant communication and that JA signals may have moved via the CMN to systemically induced defense in neighboring plants. However, when using the wild type as the donor plant and *spr2* as the receiver plant, the latter also failed to exhibit defense responses. This indicates that either the JA signal needs to be amplified in the receiver plants, or that signals different from JA induce JA biosynthesis/signaling in the receivers.

Salicylic acid (SA), another important phytohormone in disease resistance, was also suggested to be delivered via CMNs [39]. Using a two-chambered rootbox and the AM fungus *Paraglomus occultum*, Zhang et al.[39] found that *receiver* plants (*Poncirus trifoliata*) linked to donors infected for 2 days with *Xanthomonas axonopodis* had reduced expression of SA-biosynthesis genes but had elevated concentrations of SA. A 1-cm air gap was used to prevent any diffusion of signaling substances through soil and water. At a later time point (9 days post-infection) the root SA concentrations were decreased in both donor and receiver plants. Building on early findings, it was hypothesized[40] that the observed elevation in JA concentrations within both receiver and donor roots when co-inoculated with *X. axonopodis* and AM at later time points suppressed excessive SA production, as part of a potential feedback regulation.

Barto et al.[41] studied the role of CMN in allelopathic interactions between plants. Allelopathy is the phenomenon where molecules produced by a plant limit the growth of neighboring plants[42]. They showed that the presence of a CMN connected by AM fungus enhanced the accumulation of allelochemicals in receiver plants that were either applied to or released from donor plants. The allelochemicals, either the herbicide imazamox or thiophenes released by *Tagetes tenuifolia* roots, accumulated to greater concentrations in receiver plants or soils with continuous CMNs than in soils with interrupted fungal networks. This indicated that mycorrhizal hyphae can facilitate the spread of chemicals released by a plants, expanding their bioactive zone in the soil.

The first study demonstrating that signals can also be transmitted between different plant species via EcM fungi was published in 2015[43]. Using Douglas fir as the donor and Ponderosa pine as the receiver, the authors showed that both manual and insect-induced defoliation of donors resulted in increased activity of peroxidase, polyphenol oxidase, and superoxide dismutase in the receivers. Additionally, the authors found that manual defoliation of donors led to the transfer of photosynthetic C to receivers through CMNs, but not through soil or root pathways. This study also represents the first evidence of CMN-based signaling in response to mechanical damage. Subsequently, it was confirmed that signals triggered by mechanical damage can be transmitted through a CMN, activating the defense systems of receiver plants and enhancing the activity of various stress-related enzymes such as superoxide dismutase in both lucerne (*Medicago sativa*) and tomato [44,45].

Subsequent investigations used *Nicotiana attenuata*, as these plants do not respond to volatiles elicited by herbivory from neighboring individuals[46]. When grown individually, AM fungal colonization elevated concentrations of JA and jasmonoyl-isoleucine in *N. attenuata* roots, but did not affect the intensity of JA bursts in leaves elicited by leaf puncture wounds or application of oral secretions from *Manduca sexta* larvae. However, in the presence of a CMN, larger JA bursts and higher concentrations of JA metabolism-associated amino acids were detected in leaves of receiver plants. This indicated that AM fungal colonization alone did not enhance systemic defense responses, as observed in *Plantago* and *Medicago*[47], but that CMNs have the capability to transmit between interconnected plants. It was accompanied by changes in distinct defense metabolites in the leaves of the stimulated receiver plants, which led to the suggestion that CMNs may filter defense signals that are transported[46].

Potted and hydroponic experiments both have significant limitations due to the fact that the growth media for the donor and receiver plants are not separated. Consequently, there is a considerable likelihood that semiochemicals or VOCs could diffuse through the media and not via the extraradical hyphae to neighboring plants. Additionally, CMNs serve as superhighway for the transport of hyphospheric bacteria, thereby greatly expanding the effective functional space of these bacteria. These microbial networks may therefore also contribute to signal transfer between plants[48,49]. This complexity makes it challenging to distinguish whether the transmission of signals is a direct effect of a CMN, or if external, indirect factors are involved. To better differentiate between direct and indirect contributions of CMNs to signal transmission, Alaux et al.[35] used an *in-vitro* experiments in which potatoes were cultivated in physically separated compartments with their connection exclusively by the CMN and not through microbes other than AM fungi or through the diffusion of chemicals through the growth medium. This was achieved by adapting a split plate *in-vitro* cultivation system, where only fungal hyphae could cross a plastic cross wall separating the donor and receiver compartments. The donor potatoes were infected by *Phytophthora infestans*, and 24 h post-infection four defense-related genes associated with JA or ethylene signaling were significantly upregulated in the leaves of the receiver plants. No upregulation was observed in receiver plants without a CMN. In this set-up the expression of the defense-related genes returned to control concentrations after 48 h, indicating a transient response potentially priming defenses in the receiver plants.

The studies above indicate that CMNs formed by both AM fungi and EcM fungi can mediate signal transmission between plants, whether of the same or different species, induced by pathogens, herbivores and mechanical damage. Most studies have focused on AM fungi because of their extremely broad host range and prevalence in ecosystems and relevance for crop plants[50]. However, to date the nature of the signals that are transmitted are still largely unknown. Further research is needed to elucidate the nature of the signaling substances transmitted by donor plants, whether the fungi modify these signals and how the receiver plants perceive these substances to induce or prime defense responses.

3 Possible routes of signal transport via CMNs

Several hypotheses have been proposed regarding how signals may be transmitted via CMNs[51] (Fig. 1). The nature of the route impacts the speed and distance with which the signals can travel. Six possible routes are: (1) through a liquid film on the fungal hyphal surface, which is suitable for water-soluble signals, but potentially limited for long-distance transmission due to soil particle constraints[52]; (2) via diffusion through the fungal cell wall/extracellular matrix, which may be selective for non-polar molecules due to the hydrophobic nature of the cell wall[53]; (3) through diffusion within fungal hyphae, implying that signal substances need to be actively absorbed by the hyphae or passively traverse the fungal cell membrane, making the identification of membrane transporters capable of handling organic semiochemicals a crucial issue[51]; (4) aided by active transport within the fungus, (5) involve repeated cycles of secretion and uptake by the fungus, by transporters or through endocytosis and exocytosis cycles[54]; and (6) electrical signal conduction. Plants have been shown to generate electrical signals in response to mechanical damage[55], and fungi have been reported to show have spiking activity[56]. However, experimental evidence for electrical signal transmission via fungal hyphae is currently lacking. Most studies on CMNs imply a single/continuous network connecting two plants, which is often difficult to determine. In most cases, it is not possible to exclude close proximity between hyphae and plants, but not direct contact, as sufficient for signal exchange. Consequently, Rillig et al.[57] proposed the term, common fungal networks, to include networks of any

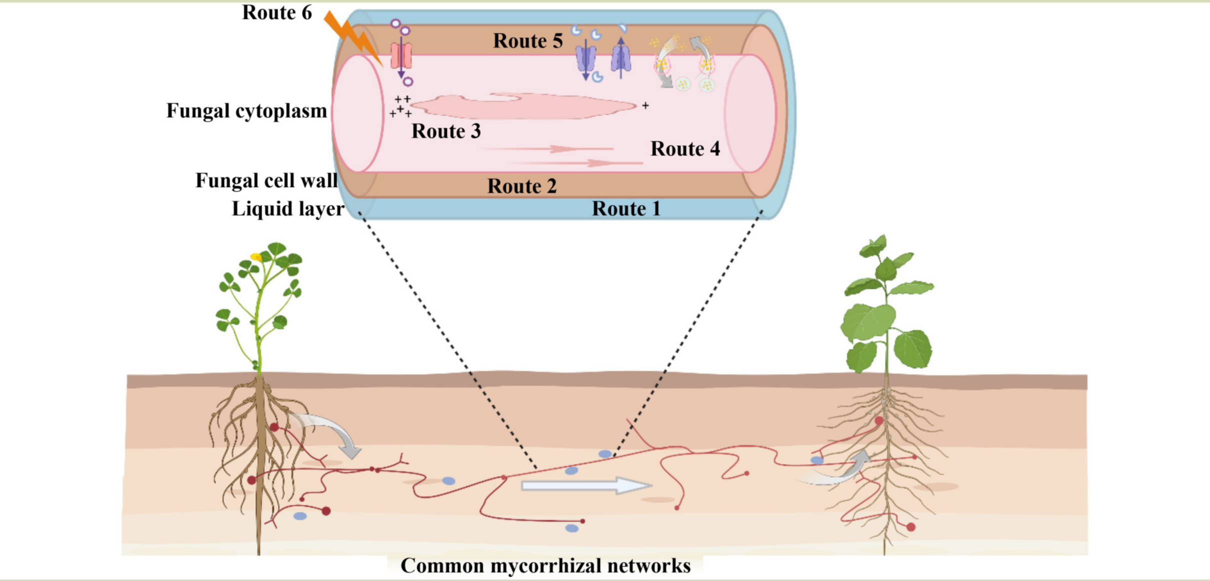


Fig. 1 Possible routes of signal transport through common mycorrhizal networks. Route 1, diffusion based transport via the liquid film surrounding hyphae; Route 2, via the extracellular matrix of hyphae; Route 3, diffusion based transport through the hyphal symplast; Route 4, active facilitated transport with hyphae; Route 5, repeated rounds of secretion and uptake, either involving specialized transporters or exocytosis/endocytosis cycles; and Route 6, electric signaling. Figure created with BioRender.com.

type of connection (direct or indirect) formed between different plants by any type of fungus.

The effectiveness of interplant signaling through CMNs in reducing the impact of pathogens and herbivores depends on the speed and distance of signal transmission. The signal must be able to reach the receiver plants and be sufficiently fast to effectively prevent them from being harmed or minimize damage to the greatest extent. Also, it has been hypothesized that different degrees of plant defense responses may be triggered based on the distance of signal transmission[58], which is ultimately determined by the resulting concentration of the signals and the affinity by which they can be perceived. This will depend on the nature of the signals transferred as well as on the transport route that they follow. Although some studies have reported responses as early as 6 h post-infection[36] the general conclusion drawn is that a response occurs in the receiver plant within 24 h of introducing pests or pathogens to the donor plant. The peak response in the receiver plant happens between 48 and 100 h post-infection[2,52,59] at interplant distances of up to 20 cm[37,38] Currently, the length of CMNs in natural settings is difficult to measure with sufficient confidence, so the maximum distance that signals can travel is currently not known. Also, a feed forward delivery of signals through CMNs between multiple plants may expand the zone of influence of a given signal[58].

4 Active versus passive transport

An important question concerning the role of CMN based communication is whether the signal transport is active or passive, and which of the partners controls the signal transmission.

Plants exude a substantial quantity of organic molecules from their roots, including plant hormones such as SA and JAs[60–62]. It is widely recognized that plants can use these exudates to recruit a (genotype) specific, beneficial microbiome to their rhizosphere and endosphere[63–65]. The composition of root exudates can further change depending on developmental stage and environmental conditions[66,67] and it is thought that plants can recruit for beneficial microbes depending on their needs. For example, under phosphate limiting conditions more strigolactones are exuded to attract AM fungi[68,69]. Also, more organic acids are exuded which can be a C source for certain beneficial bacteria. For example, oxalotrophy is associated with the successful colonization of plant-beneficial species of the genus *Burkholderia*[70]. Castrillo et al.[71] showed that crosstalk between the plant immune system and nutrient demands helps to shape the root microbiome. Although many compounds may be passively exuded due to concentration differences between the plant cytoplasm and the soil environment, it is clear that the plant actively controls the nature and amount of chemicals released from its roots.

4.1 Passive transport

In the case of passive transport through the CMN, the chemicals exuded by plant roots can travel via diffusion-based (concentration-dependent) mechanisms either along the liquid film on the fungal outer surface (Route 1, Fig. 1) or the fungal cell wall (Route 2). In water, diffusion coefficients are typically in the range of 10^{-10} to 10^{-9} $m^2 \cdot s^{-1}$[72,73]. In a liquid film this transport may be accelerated due to convection. Also, it is theoretically possible that exudates of the fungus increase the diffusion speed of molecules derived from the plant. However, interactions with soil particles or bacteria closely associated with the fungal hyphae may decrease the effective spread of the signals. If these molecules are taken up by the fungi, they may also diffuse through the cytoplasm of the hyphae (Route 3). In this case, cytoplasmic movements may enhance the speed with which the compounds diffuse, particularly in the coenocytic AM fungi, where cytoplasmic streaming is an important feature.

4.2 Active transport

Active transport by the fungus (Routes 4 and 5) would involve transport against a concentration gradient or in a directed manner to different parts of the fungal network. Currently there is no evidence that the fungi direct the transport of semiochemicals. However, recently fluorescent quantum-dot nanoparticles (QD-apatite) were used to track their uptake and distribution in a AM fungal network connecting older versus younger roots in an *in-vitro* carrot root culture system[74]. It was shown that more QD-apatite was taken up (likely via endocytosis) and transferred to young roots under low-P conditions, suggesting that the fungus can direct more P to hosts with a higher nutrient demand. The molecular mechanism that control such differential allocation of nutrients within the network are still unknown. It was also shown that an AM fungus can adapt its transcriptome locally in a fungal network[75], which may locally affect hyphal transport. Evidence for an active role of the fungus in transporting and distributing of semiochemicals in the CMN will require the development and implementation of advanced labeling strategies, possibly in combination with nano-SIMS (nanoscale secondary ion mass spectrometry) or nano-particle tracking.

5 Network benefits

From a plant-centric perspective, the benefits of receiving signals are evident for the receiver; it can induce the occurrence of defensive responses, protecting the receivers from potential diseases or pest invasions. The cost of disease invasion is much greater than the cost of priming or inducing an immune response[76,77]. However, the benefits of actively sending signals are somewhat challenging to understand for the donor. Gilbert and Johnson[2,52] suggested that if relatives are closely related and connected by the same CMN, it may increase the inclusive fitness of the donor (i.e., its gene pool includes adaptations of its family) to warn relatives of imminent pest attacks. Also, different plants may have different potential to ward off enemies or to recruit beneficial microbes, which could be an incentive to share signals also with non-kin plants. In the case of allelopathic signals, an expanded zone of influence would also be beneficial for the donor plants to reduce competition for resources by neighboring plants.

Babikova et al.[58] took a fungal-centric approach to consider the potential adaptive benefits of fungal networks in aiding plant signal transmission. They proposed that within this integrated system fungi gain greater benefits, specifically C, at minimal cost. They hypothesized that if fungi could control the strength and direction of signals, they would allocate signals to the most advantageous C sources or to those plants that, after receiving these signals, could better use them to protect themselves. Johnson and Gilbert[52] further substantiated this viewpoint[52]. They highlighted that in stable environments, such as grasslands or forests, where CMNs persist over the long-term, fungi a negatively impacted if they lose a host plant with which they have established a stable and enduring cooperation due to disease or pests. Consequently, they may can advantage by transmitting warning signals. Therefore, attempting to control signals for direct benefit could be advantageous for any partner involved.

6 Conclusions and outlook

It has become clear that plants can use CMNs for communication, enhancing their protection and adaptability, which may be an essential strategy in sustainable and nutrient-efficient ecosystems.

However, the experimental confirmation that plants communicate through CMNs is not as straightforward as initially thought. Especially in more natural settings, it is crucial to ensure that plants are connected through the same CMN, a challenge addressable by analyzing genetic markers of fungi in roots[2]. However, a direct comparison between plants infected by mycorrhizal fungi and those not infected can be misleading. Fungal colonization affects plant metabolism and signal transduction, altering, for example, the quantity and composition of its VOCs[58,78], its nutritional demands and immune responses, and thereby its overall fitness. Therefore, proper controls and meticulous experiments need to be designed to take such possible indirect effects into account.

A major question is whether CMN-based communication can be actively managed to enhance the ability of both plant and fungus to tolerate environmental challenges. Therefore, elucidating the nature of signals transmitted through CMNs and understanding the mechanisms of signal transmission will be of key importance. Some recommended research directions include: (1) identifying the specific signal molecules involved and their chemical properties; (2) investigating the mechanisms and pathways of signal transmission within CMNs; (3) exploring the temporal and spatial dynamics of signal exchange; (4) examining the regulatory factors influencing signal production, release, transmission and reception; (5) comparing signal transmission mechanisms among different types of mycorrhizal associations; and (6) characterizing the specificity of signal exchange between various fungal and plant species.

The development of cutting-edge technology, including single particle tracking together microfluidics devices[79] and advances in single (live) cell spatial metabolomics[80], are expected to enable a comprehensive study of the transmission of signals via CMNs.

Finally, most studies on CMNs have focused on the transport of signals between plants. However, there is increasing attention for the role of mycorrhizal fungi in shaping the soil microbiome[81]. For example, fructose exuded by the AM fungus *Rhizophagus irregularis* was found to stimulate organic phosphate mineralization by the phosphate-solubilizing bacteria *Rahnella aquatilis*, which resides in the hyphosphere of the fungus[82]. Given the potential diversity of signals sent by plants to influence the soil microbiome, it will be important to investigate how microbial networks influence interplant communication.

Acknowledgements

Xiaofan Ma is supported by the China Scholarship Council (201913043).

Compliance with ethics guidelines

Xiaofan Ma and Erik Limpens declare that they have no conflicts of interest or financial conflicts to disclose. This article does not contain any studies with human or animal subjects performed by any of the authors.

REFERENCES

1. Smith S E, Read D J. Introduction. In: Smith S E, Read D, eds. Mycorrhizal Symbiosis. 2nd ed. London: *Academic press*, 2010, 1–10
2. Gilbert L, Johnson D. Plant-plant communication through common mycorrhizal networks. *Advances in Botanical Research*, 2017, **82**: 83–97
3. Massicotte H B, Peterson R, Ackerley C, Piché Y. Structure and ontogeny of *Alnus crispa–Alpova diplophloeus* ectomycorrhizae. *Canadian Journal of Botany*, 1986, **64**(1): 177–192
4. Gutjahr C, Parniske M. Cell and developmental biology of arbuscular mycorrhiza symbiosis. *Annual Review of Cell and Developmental Biology*, 2013, **29**(1): 593–617
5. Maya M A, Matsubara Y I. Influence of arbuscular mycorrhiza on the growth and antioxidative activity in cyclamen under heat stress. *Mycorrhiza*, 2013, **23**(5): 381–390
6. Van Wees S C, Van Der Ent S, Pieterse C M. Plant immune responses triggered by beneficial microbes. *Current Opinion in Plant Biology*, 2008, **11**(4): 443–448
7. Helgason T, Daniell T, Husband R, Fitter A H, Young J. Ploughing up the wood-wide web. *Nature*, 1998, **394**(6692): 431
8. Karst J, Jones M D, Hoeksema J D. Positive citation bias and overinterpreted results lead to misinformation on common mycorrhizal networks in forests. *Nature Ecology & Evolution*, 2023, **7**(4): 501–511
9. Henriksson N, Marshall J, Högberg M, Högberg P, Polle A, Franklin O, Näsholm T. Re-examining the evidence for the mother tree hypothesis—Resource sharing among trees via ectomycorrhizal networks. *New Phytologist*, 2023, **239**(1): 19–28
10. Klein T, Rog I, Livne-Luzon S, Van Der Heijden M G A, Körner C. Belowground carbon transfer across mycorrhizal networks among trees: facts, not fantasy. *Open Research Europe*, 2023, **3**: 168
11. Robinson D, Fitter A. The magnitude and control of carbon transfer between plants linked by a common mycorrhizal network. *Journal of Experimental Botany*, 1999, **50**(330): 9–13

12. Vohník M, Sadowsky J J, Kohout P, Lhotáková Z, Nestby R, Kolařík M. Novel root-fungus symbiosis in Ericaceae: sheathed ericoid mycorrhiza formed by a hitherto undescribed basidiomycete with affinities to Trechisporales. *PLoS One*, 2012, **7**(6): e39524
13. Leake J, Johnson D, Donnelly D, Muckle G, Boddy L, Read D. Networks of power and influence: the role of mycorrhizal mycelium in controlling plant communities and agroecosystem functioning. *Canadian Journal of Botany*, 2004, **82**(8): 1016–1045
14. Chagnon P L. Ecological and evolutionary implications of hyphal anastomosis in arbuscular mycorrhizal fungi. *FEMS Microbiology Ecology*, 2014, **88**(3): 437–444
15. Taylor A F. Common mycelial networks: life-lines and radical addictions. *New Phytologist*, 2006, **169**(1): 6–8
16. Egerton-Warburton L M, Querejeta J I, Allen M F. Common mycorrhizal networks provide a potential pathway for the transfer of hydraulically lifted water between plants. *Journal of Experimental Botany*, 2007, **58**(6): 1473–1483
17. Finlay R, Read D. The structure and function of the vegetative mycelium of ectomycorrhizal plants: I. Translocation of ^{14}C-labelled carbon between plants interconnected by a common mycelium. *New Phytologist*, 1986, **103**(1): 143–156
18. Van Der Heijden M G, Horton T R. Socialism in soil? The importance of mycorrhizal fungal networks for facilitation in natural ecosystems. *Journal of Ecology*, 2009, **97**(6): 1139–1150
19. Cardini A, Pellegrino E, Declerck S, Calonne-Salmon M, Mazzolai B, Ercoli L. Direct transfer of zinc between plants is channelled by common mycorrhizal network of arbuscular mycorrhizal fungi and evidenced by changes in expression of zinc transporter genes in fungus and plant. *Environmental Microbiology*, 2021, **23**(10): 5883–5900
20. Bago B, Zipfel W, Williams R M, Jun J, Arreola R, Lammers P J, Pfeffer P E, Shachar-Hill Y. Translocation and utilization of fungal storage lipid in the arbuscular mycorrhizal symbiosis. *Plant Physiology*, 2002, **128**(1): 108–124
21. Cabral C, Wollenweber B, António C, Rodrigues A M, Ravnskov S. Aphid infestation in the phyllosphere affects primary metabolic profiles in the arbuscular mycorrhizal hyphosphere. *Scientific Reports*, 2018, **8**(1): 14442
22. Kachroo A, Kachroo P. Mobile signals in systemic acquired resistance. *Current Opinion in Plant Biology*, 2020, **58**: 41–47
23. Hodge A, Storer K. Arbuscular mycorrhiza and nitrogen: implications for individual plants through to ecosystems. *Plant and Soil*, 2015, **386**(1–2): 1–19
24. Walder F, Niemann H, Natarajan M, Lehmann M F, Boller T, Wiemken A. Mycorrhizal networks: common goods of plants shared under unequal terms of trade. *Plant Physiology*, 2012, **159**(2): 789–797
25. Fellbaum C R, Mensah J A, Cloos A J, Strahan G E, Pfeffer P E, Kiers E T, Bücking H. Fungal nutrient allocation in common mycorrhizal networks is regulated by the carbon source strength of individual host plants. *New Phytologist*, 2014, **203**(2): 646–656
26. Kiers E T, Duhamel M, Beesetty Y, Mensah J A, Franken O, Verbruggen E, Fellbaum C R, Kowalchuk G A, Hart M M, Bago A, Palmer T M, West S A, Vandenkoornhuyse P, Jansa J, Bücking H. Reciprocal rewards stabilize cooperation in the mycorrhizal symbiosis. *Science*, 2011, **333**(6044): 880–882
27. Noë R, Hammerstein P. Biological markets. *Trends in Ecology & Evolution*, 1995, **10**(8): 336–339
28. Schwartz M W, Hoeksema J D. Specialization and resource trade: biological markets as a model of mutualisms. *Ecology*, 1998, **79**(3): 1029–1038
29. Weremijewicz J, Janos D P. Common mycorrhizal networks amplify size inequality in *Andropogon gerardii* monocultures. *New Phytologist*, 2013, **198**(1): 203–213
30. Bennett A E, Groten K. The costs and benefits of plant-arbuscular mycorrhizal fungal interactions. *Annual Review of Plant Biology*, 2022, **73**(1): 649–672
31. Figueiredo A F, Boy J, Guggenberger G. Common mycorrhizae network: a review of the theories and mechanisms behind underground interactions. *Frontiers in Fungal Biology*, 2021, **2**: 735299
32. Luo X, Liu Y N, Li S Y, He X H. Interplant carbon and nitrogen transfers mediated by common arbuscular mycorrhizal networks: beneficial pathways for system functionality. *Frontiers in Plant Science*, 2023, **14**: 1169310
33. Chamberlain K, Guerrieri E, Pennacchio F, Pettersson J, Pickett J A, Poppy G M, Powell W, Wadhams L J, Woodcock C M. Can aphid-induced plant signals be transmitted aerially and through the rhizosphere. *Biochemical Systematics and Ecology*, 2001, **29**(10): 1063–1074
34. Dicke M, Dijkman H. Within-plant circulation of systemic elicitor of induced defence and release from roots of elicitor that affects neighbouring plants. *Biochemical Systematics and Ecology*, 2001, **29**(10): 1075–1087
35. Alaux P L, Naveau F, Declerck S, Cranenbrouck S. Common mycorrhizal network induced JA/ET genes expression in healthy potato plants connected to potato plants infected by *Phytophthora infestans*. *Frontiers in Plant Science*, 2020, **11**: 602
36. Song Y Y, Ye M, Li C Y, He X H, Zhu-Salzman K, Wang R L, Su Y J, Luo S M, Zeng R S. Hijacking common mycorrhizal networks for herbivore-induced defence signal transfer between tomato plants. *Scientific Reports*, 2014, **4**(1): 3915
37. Song Y Y, Zeng R S, Xu J F, Li J, Shen X, Yihdego W G. Interplant communication of tomato plants through underground common mycorrhizal networks. *PLoS One*, 2010, **5**(10): e13324
38. Babikova Z, Gilbert L, Bruce T J, Birkett M, Caulfield J C, Woodcock C, Pickett J A, Johnson D. Underground signals carried through common mycelial networks warn neighbouring plants of aphid attack. *Ecology Letters*, 2013, **16**(7): 835–843
39. Zhang Y C, Zou Y N, Liu L P, Wu Q S. Common mycorrhizal networks activate salicylic acid defense responses of trifoliate orange (*Poncirus trifoliata*). *Journal of Integrative Plant Biology*, 2019, **61**(10): 1099–1111

40. Zhang Y C, Liu L P, Zou Y N, Liu C Y, Wu Q S. Responses of signal substances to canker in trifoliate orange roots through mycorrhizal hyphal bridge. *Mycosystema*, 2017, **36**(7): 1028-1036 (in Chinese)
41. Barto E K, Hilker M, Müller F, Mohney B K, Weidenhamer J D, Rillig M C. The fungal fast lane: common mycorrhizal networks extend bioactive zones of allelochemicals in soils. *PLoS One*, 2011, **6**(11): e27195
42. Inderjit, Weston L A, Duke S O. Inderjit, Weston L A, Duke S O. Challenges, achievements and opportunities in allelopathy research. *Journal of Plant Interactions*, 2005, **1**(2): 69–81
43. Song Y Y, Simard S W, Carroll A, Mohn W W, Zeng R S. Defoliation of interior Douglas-fir elicits carbon transfer and stress signalling to ponderosa pine neighbors through ectomycorrhizal networks. *Scientific Reports*, 2015, **5**(1): 8495
44. Li S, Sina Y Z, Xu R, Zi S H, Fan L Y, Liu T. Defense signal transmission between alfalfa plants through underground mycorrhizal network. *Journal of Tropical and Subtropical Botany*, 2021, **29**(4): 382–388 (in Chinese)
45. Lian F Z, Lin Y B, Hu L, Wang J, Ceng R S, Song Y Y. Transfer of mechanical wounding signaling between tomato plants through common mycorrhizal networks. *Journal of Fujian Agriculture and Forestry University (Natural Science Edition)*, 2019, **48**(1): 9–15 (in Chinese)
46. Song Y Y, Wang M, Zeng R S, Groten K, Baldwin I T. Priming and filtering of antiherbivore defences among *Nicotiana attenuata* plants connected by mycorrhizal networks. *Plant, Cell & Environment*, 2019, **42**(11): 2945–2961
47. Schweiger R, Baier M C, Persicke M, Müller C. High specificity in plant leaf metabolic responses to arbuscular mycorrhiza. *Nature Communications*, 2014, **5**(1): 3886
48. Jiang F Y, Zhang L, Zhou J C, George T S, Feng G. Arbuscular mycorrhizal fungi enhance mineralisation of organic phosphorus by carrying bacteria along their extraradical hyphae. *New Phytologist*, 2021, **230**(1): 14–16
49. de Novais C B, Sbrana C, Da Conceição Jesus E, Rouws L F M, Giovannetti M, Avio L, Siqueira J O, Saggin O J Junior, Da Silva E M R, De Faria S M. Mycorrhizal networks facilitate the colonization of legume roots by a symbiotic nitrogen-fixing bacterium. *Mycorrhiza*, 2020, **30**(2–3): 389–396
50. Tedersoo L, Bahram M, Zobel M. How mycorrhizal associations drive plant population and community biology. *Science*, 2020, **367**(6480): eaba1223
51. Barto E K, Weidenhamer J D, Cipollini D, Rillig M C. Fungal superhighways: do common mycorrhizal networks enhance below ground communication. *Trends in Plant Science*, 2012, **17**(11): 633–637
52. Johnson D, Gilbert L. Interplant signalling through hyphal networks. *New Phytologist*, 2015, **205**(4): 1448–1453
53. Allen M F. Mycorrhizal fungi: highways for water and nutrients in arid soils. *Vadose Zone Journal*, 2007, **6**(2): 291–297
54. van't Padje A, Werner G D, Kiers E T. Mycorrhizal fungi control phosphorus value in trade symbiosis with host roots when exposed to abrupt 'crashes' and 'booms' of resource availability. *New Phytologist*, 2021, **229**(5): 2933–2944
55. Mousavi S A, Chauvin A, Pascaud F, Kellenberger S, Farmer E E. GLUTAMATE RECEPTOR-LIKE genes mediate leaf-to-leaf wound signalling. *Nature*, 2013, **500**(7463): 422–426
56. Andrew A. Language of fungi derived from their electrical spiking activity. *Royal Society Open Science*, 2022, **9**(4): 211926
57. Rillig M C, Lehmann A, Lanfranco L, Caruso T, Johnson D. Clarifying the definition of common mycorrhizal networks. *Functional Ecology*, 2024, **00**: 1–7
58. Babikova Z, Johnson D, Bruce T, Pickett J, Gilbert L. Underground allies: how and why do mycelial networks help plants defend themselves? What are the fitness, regulatory, and practical implications of defence-related signaling between plants via common mycelial networks. *BioEssays*, 2014, **36**(1): 21–26
59. Babikova Z, Johnson D, Bruce T, Pickett J, Gilbert L. How rapid is aphid-induced signal transfer between plants via common mycelial networks. *Communicative & Integrative Biology*, 2013, **6**(6): 835–843
60. Jacoby R P, Koprivova A, Kopriva S. Pinpointing secondary metabolites that shape the composition and function of the plant microbiome. *Journal of Experimental Botany*, 2021, **72**(1): 57–69
61. Lebeis S L, Paredes S H, Lundberg D S, Breakfield N, Gehring J, Mcdonald M, Malfatti S, Glavina Del Rio T, Jones C D, Tringe S G, Dangl J L. Salicylic acid modulates colonization of the root microbiome by specific bacterial taxa. *Science*, 2015, **349**(6250): 860–864
62. Lopes L D, Wang P, Futrell S L, Schachtman D P. Sugars and jasmonic acid concentration in root exudates affect maize rhizosphere bacterial communities. *Applied and Environmental Microbiology*, 2022, **88**(18): e00971–22
63. Santoyo G. How plants recruit their microbiome? New insights into beneficial interactions. *Journal of Advanced Research*, 2022, **40**: 45–58
64. Wen T, Zhao M L, Yuan J, Kowalchuk G A, Shen Q R. Root exudates mediate plant defense against foliar pathogens by recruiting beneficial microbes. *Soil Ecology Letters*, 2021, **3**(1): 42–51
65. Huang X F, Chaparro J M, Reardon K F, Zhang R F, Shen Q R, Vivanco J M. Rhizosphere interactions: root exudates, microbes, and microbial communities. *Botany*, 2014, **92**(4): 267–275
66. Canarini A, Kaiser C, Merchant A, Richter A, Wanek W. Root exudation of primary metabolites: mechanisms and their roles in plant responses to environmental stimuli. *Frontiers in Plant Science*, 2019, **10**: 422679
67. Vives-Peris V, Lopez-Climent M F, Perez-Clemente R M, Gomez-Cadenas A. Root involvement in plant responses to adverse environmental conditions. *Agronomy*, 2020, **10**(7): 942
68. Yoneyama K, Xie X N, Kim H I, Kisugi T, Nomura T, Sekimoto H, Yokota T, Yoneyama K. How do nitrogen and phosphorus deficiencies affect strigolactone production and

exudation. *Planta*, 2012, **235**(6): 1197–1207

69. Yoneyama K, Yoneyama K, Takeuchi Y, Sekimoto H. Phosphorus deficiency in red clover promotes exudation of orobanchol, the signal for mycorrhizal symbionts and germination stimulant for root parasites. *Planta*, 2007, **225**(4): 1031–1038
70. Kost T, Stopnisek N, Agnoli K, Eberl L, Weisskopf L. Oxalotrophy, a widespread trait of plant-associated *Burkholderia* species, is involved in successful root colonization of lupin and maize by *Burkholderia phytofirmans*. *Frontiers in Microbiology*, 2014, **4**: 70529
71. Castrillo G, Teixeira P J P L, Paredes S H, Law T F, de Lorenzo L, Feltcher M E, Finkel O M, Breakfield N W, Mieczkowski P, Jones C D, Paz-Ares J, Dangl J L. Root microbiota drive direct integration of phosphate stress and immunity. *Nature*, 2017, **543**(7646): 513–518
72. Ferrell R T, Himmelblau D M. Diffusion coefficients of nitrogen and oxygen in water. *Journal of Chemical & Engineering Data*, 1967, **12**(1): 111–115
73. Lead J R, Starchev K, Wilkinson K J. Diffusion coefficients of humic substances in agarose gel and in water. *Environmental Science & Technology*, 2003, **37**(3): 482–487
74. van't Padje A, Oyarte Galvez L, Klein M, Hink M A, Postma M, Shimizu T, Kiers E T. Temporal tracking of quantum-dot apatite across in vitro mycorrhizal networks shows how host demand can influence fungal nutrient transfer strategies. *ISME Journal*, 2021, **15**(2): 435–449
75. Zeng T, Holmer R, Hontelez J, Te Lintel-Hekkert B, Marufu L, De Zeeuw T, Wu F Y, Schijlen E, Bisseling T, Limpens E. Host- and stage-dependent secretome of the arbuscular mycorrhizal fungus *Rhizophagus irregularis*. *Plant Journal*, 2018, **94**(3): 411–425
76. Suza W P, Avila C A, Carruthers K, Kulkarni S, Goggin F L, Lorence A. Exploring the impact of wounding and jasmonates on ascorbate metabolism. *Plant Physiology and Biochemistry*, 2010, **48**(5): 337–350
77. Babikova Z, Gilbert L, Bruce T, Dewhirst S Y, Pickett J A, Johnson D. Arbuscular mycorrhizal fungi and aphids interact by changing host plant quality and volatile emission. *Functional Ecology*, 2014, **28**(2): 375–385
78. Fontana A, Reichelt M, Hempel S, Gershenzon J, Unsicker S B. The effects of arbuscular mycorrhizal fungi on direct and indirect defense metabolites of *Plantago lanceolata* L. *Journal of Chemical Ecology*, 2009, **35**(7): 833–843
79. O'Callaghan J A, Kamat N P, Vargo K B, Chattaraj R, Lee D, Hammer D A. A microfluidic platform for the synthesis of polymer and polymer-protein-based protocells. *European Physical Journal E*, 2024, **47**(6): 37
80. Lanekoff I, Sharma V V, Marques C. Single-cell metabolomics: where are we and where are we going. *Current Opinion in Biotechnology*, 2022, **75**: 102693
81. Zhang L, Zhou J C, George T S, Limpens E, Feng G. Arbuscular mycorrhizal fungi conducting the hyphosphere bacterial orchestra. *Trends in Plant Science*, 2022, **27**(4): 402–411
82. Zhang L, Feng G, Declerck S. Signal beyond nutrient, fructose, exuded by an arbuscular mycorrhizal fungus triggers phytate mineralization by a phosphate solubilizing bacterium. *ISME Journal*, 2018, **12**(10): 2339–2351