INTERPLANT COMMUNICATION FACILITATED BY COMMON MYCORRHIZAL NETWORKS

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Bachelor thesis

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Summary

Most plants establish symbiotic relationships with mycorrhizal fungi in order to gather essential nutrients. In recent decades, mycorrhizal fungi have frequently been shown to interconnect plants by forming common mycorrhizal networks (CMN). One of the functions that CMNs can facilitate is the transfer of signals between plants. Several lab studies have shown interplant signal transfer via CMNs, but none have yet identified the nature of these signals. There is evidence that at least part of the signal is chemical in nature and electrical signals might also play a role. Opinion among researchers is divided on the question which partner, plant or fungus, is in control of the signal. Some point to evidence of kin selection in plants through CMNs and argue for a phytocentric (plant-centric) view, while others take a mycocentric (fungus-centric) view and think that fungi mainly control the signals for their own gain. Not all experts are convinced that CMNs are ecologically significant. The criticisms raised by these researchers will have to be addressed by first identifying the signal that is sent between plants through CMNs. Promising approaches for identifying this signal include genetically engineering strains of fungi that are unable to synthesize certain compounds and measuring plant responses to electrical signals transmitted through CMNs. Once the signal is identified, it should be easier to design experiments that can better test the ecological significance interplant signalling through CMNs.

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1. Background on common mycorrhizal networks

Symbioses between plants and fungi have been known since at least the middle of the nineteenth century. Charles Darwin was among the first to suggest that orchids might parasitize on fungi as seedlings, writing to a colleague that he had "not a fact to go on" but had "a firm conviction" that germinating orchid seeds "are parasites in early youth on cryptogams [or fungi]" (Darwin, 1863). Darwin would be proven right 36 years later when fungi were shown to be essential for orchid seedling germination (Selosse *et al*., 2011). In the decades since then, many advancements have been made in this field. Mutualistic plant-fungal symbioses were called mycorrhizas (meaning 'fungal root') and several types were identified. One of the most common types is arbuscular mycorrhiza, where fungal hyphae penetrate the cell walls of plant roots. Ectomycorrhiza, where fungi grow in between plant root cells but do not penetrate them, are most prevalent among woody plants. Mycorrhizae are formed by over 90% of all land plants and are often critical for the survival of both the plants and fungi involved. Plants supply fungi with carbohydrates formed during photosynthesis and fungi supply plants with nutrients gathered from the soil. In short, fungi are essential for the survival of most land plants. Fossil evidence has shown that mycorrhizal associations between plants and fungi go back hundreds of millions of years. Furthermore, the first land plants had not yet evolved roots and likely depended on fungi to act as their root system to absorb water and nutrients (Strullu-Derrien, Selosse, Kenrick, and Martin, 2018).

The first hints that carbon might pass between plants via a fungal pathway came when researchers started to take a closer look at mycoheterotrophs. These are plants that do not produce chlorophyl but rely entirely on fungi for their carbon. The genus *Monotropa* was the focus of much research early on. As far back as 1882, a Russian botanist named F. Kamienski speculated that substances might move between these plants via fungal connections (Trappe, 2015). This speculation was apparently not noticed for a long time, and the next major discovery came in 1960. In that year, sugars were shown to move from trees to nearby *Monotropa* plants by Swedish Botanist Erik Björkman. He injected the trees with radioactive sugars and showed that these sugars accumulated in nearby *Monotropa* plants (Björkman, 1960). This was the first demonstration that substances can pass between plants through a common mycorrhizal network (CMN).

This kind of transfer between plants through CMNs had still only been shown between mycoheterotrophic plants. Since studies on *Monotropa,* researchers had hypothesised that transfer of carbon was also possible between green plants, and this was confirmed by Francis and Read (1984). They grew "donor" and "receiver" plants next to each other, either with or without mycorrhizae. Donor plants were fed with radioactive CO_2 and both the donor and receiver plants were harvested. The roots of both plants were then exposed to radiographic film. When mycorrhizae were present, radioactivity was visible in the donor, the fungus and the receiver. When no mycorrhizae were present, radioactivity was only visible in the donor plant. This study conclusively showed that carbon can pass between green plants through a CMN in a laboratory setting.

It wasn't until 1997 that transfer of carbon between green plants in nature was first demonstrated by Suzanne Simard and her colleagues. Bidirectional and net carbon transfer between the ectomycorrhizal tree species *Betula papyrifera* and *Pseudotsuga menziesii* was demonstrated in field conditions (Simard *et al*., 1997). A third species with arbuscular mycorrhizae, *Thuja plicata*, was used as a control. Pairs of seedlings of these species were exposed to radioactive carbon isotopes. After two years carbon had passed from *B. papyrifera* to *P. menziesii*, which shared a mycorrhizal network, but much less between *B. papyrifera* and *T. plicata*, which did not. The amount of carbon transferred to *P. menziesii* was on average 6% of the carbon taken up by *B. papyrifera*, a number which Simard *et al*. (1997) deemed meaningful. In other words, this amount of carbon could make a difference for the

survival of *P. menziesii*. This study has been very influential and inspired much of the subsequent research that has been done on CMNs. The most common term used for CMNs outside of scientific literature, "wood wide web", comes from a commentary on this study by Sir David Read (1997).

Interplant communication is also possible through a CMN composed of AM fungi, and this was first demonstrated by Song *et al*. (2010). They compared 'donor' plants, which had received a pathogenic fungus, with healthy 'receiver' plants in mycorrhizal and non-mycorrhizal conditions. The receiver plants that were connected to the donor plants by a CMN were shown to become more disease resistant and activate several defence-related enzymes and genes. Subsequent studies confirmed these findings and showed that signals warning of insect attacks could also be passed between plants via CMNs (Babikova *et al*., 2013a; Song *et al*.,2014; Song *et al*., 2015; Song *et al*., 2019; Yu *et al*., 2022)(figure 1). Receiver plants in these studies were shown to activate defence-related enzymes and produce volatile organic compounds (VOCs) that would attract herbivore enemies such as parasitoid wasps. Of these studies, the one by Song *et al*. (2015) is notable because it showed for the first time that signals can be sent through EM networks between different species. Previous studies had focussed on AM networks.
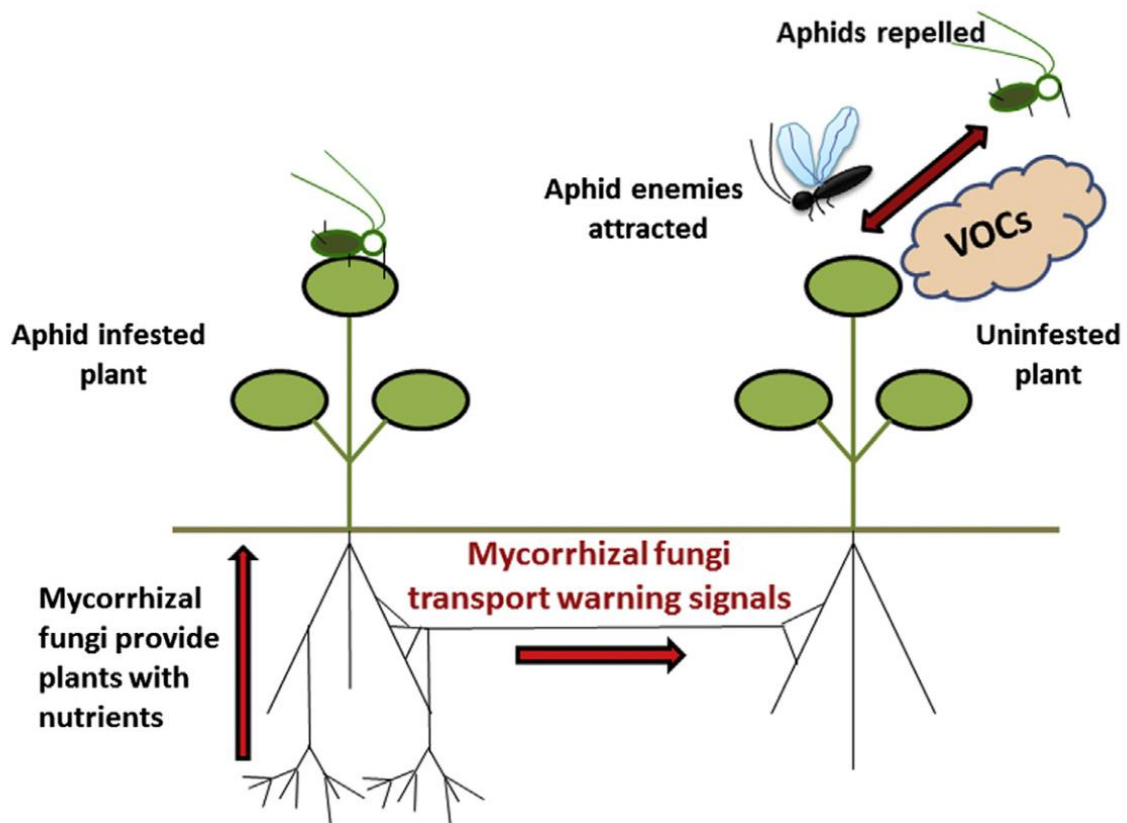
Figure 1. Schematic overview of CMN-mediated interplant signal transfer. An aphid-infested plant can send a warning signal to a healthy plant through a CMN. The healthy plant responds by producing volatile organic compounds that attract parasitoid wasps which feed on aphids (Gilbert and Johnson, 2017).

CMNs are expected to be common across the globe and can potentially influence ecosystem functioning on a large scale. Carbon and nutrient transfer through CMNs have been discussed much in the literature but are not the focus of this review. In the following section I discuss theories about potential mechanisms and evolutionary implications of interplant signal transfer through CMNs.

2. Theories about functioning and implications of CMN signal transfer

2.1. Potential mechanisms behind CMN signal transfer

The discovery of CMN-mediated interplant signals is very recent and at the time of writing, the exact signalling mechanism has not yet been identified. Johnson and Gilbert (2014) identified three possible mechanisms by which CMNs could enable interplant signalling:

1. Transport of molecules in liquid films on the external surface of hyphae via capillary action or microbes.
2. Delivery of signal molecules via cytoplasmic streaming within hyphae.
3. Conduits for wound-induced electrical signals.

Mechanism 1 is unlikely due to close interaction of fungal hyphae with soil particles, which makes transport of water inefficient. Transfer of signals over large enough distances and at fast enough speeds to deter herbivory in neighbouring plants via mechanism 1 is therefore likely not possible. There is some evidence that electrical potentials affect interplant signalling through CMNs (mechanism 3), and both fungi and plants can respond to these potentials (Wildon *et al.*,1992; Olsson.,1999). AM fungi have been measured to influence electrical signals in roots of leek (*Allium ampeloprasum*) in one study (Ayling *et al.*, 1997). Interestingly, it was recently demonstrated that mycelium-mediated interplant signal transfer can occur through electrical signals (Thomas and Cooper., 2022). Pairs of seedlings (*Pisum sativum* and *Cucumis sativus*) inoculated with mycorrhizal fungi were grown on agar plates. There was a small gap between these agar plates and the mycelium was forced to bridge this gap. This ensured that an electrical signal travelled through the mycelium and not through agar. Leaves of donor plants were then damaged by clipping, which would incite an electrical response in the donor. This electrical signal could reliably travel from the donor, through the mycelium bridge into the receiver plant. However, the authors did not test for any physiological response in receiver plants. Thus, it remains to be shown that plants can respond to these electrical signals by producing defence enzymes or volatile organic compounds to deter herbivory.

Cytoplasmic streaming within hyphae seems like another logical mechanism for interplant signal exchange, given that it is known that sugars, lipids and amino acids can be exchanged between mycorrhizal fungi and plants (Smith and Read. 2008). It would not be much of a stretch to extend this signal pathway from plant-fungus to plant-fungus-plant. Johnson and Gilbert (2014) therefore identify mechanism 2 to be most likely to enable interplant signalling through CMNs.

Alternatively, the signal might consist of different substances that travel between plants via CMNs. Signal molecules transmitted across CMNs may not cross over from root to fungus (Rasheed *et al.*, 2022). Rather, these molecules might incite the fungus to produce its own signal, which is later picked up by the receiver plant. The nature of the signals in both plants and fungi remains unknown, but there are promising candidates. The jasmonate pathway is a probable mechanism of defence signal transduction in plants. This pathway consists of various signalling molecules known as jasmonates that, among other functions, regulate plant wound response. Song *et al.* (2014) demonstrated that donor plants with mutations that made them unable to synthesize jasmonates were unable to induce defence responses in receiving plants. On the other hand, donors with intact jasmonate pathways were able to induce defence responses. Song *et al.* (2014) did not prove that jasmonates travelled through CMNs, yet despite what Rasheed *et al.* (2022) suggest this remains a possibility. The fungal signal that travels through the CMN remains unclear.

Most of the available literature suggests that chemical transfer via cytoplasmic streaming through hyphae is the most likely mechanism for interplant signal exchange through CMNs. This seems to be because this type of transfer is already well studied as part of mycorrhizal associations. The chemical jasmonate pathway is known to be important in signal transfer within plants, but it is unknown if jasmonates can also travel through CMNs. The alternative action potential mechanism is much less studied than chemical transfer mechanisms, although given what is known about both mechanisms, they seem to me equally likely to facilitate interplant signalling at least in part. Alternatively, the two mechanisms may not be mutually exclusive and could both contribute to interplant signal transfer (Gilbert and Johnson., 2017).

Ultimately, experiments will have to be conducted to uncover the mechanism whereby interplant signals are sent. I discuss potential experimental designs in section 3.

2.2. Possible benefits of CMN signal transfer for plants and fungi

If interplant signalling through CMNs happens on a large scale in nature, this could have profound evolutionary implications for the plants, fungi and insects involved. There has been debate in the literature about the question which partner, the plant or the fungus, is in control of the signal, and whether a signal is actively being sent or not. Some researchers take a phytocentric (plant-centric) viewpoint and argue that plants are actively sending warning signals about insects to their offspring as a form of kin selection. Others take a mycocentric (fungus-centric) viewpoint and argue that the fungal partner is in control of where a signal is being sent and distributes the signal across a CMN to those plants that it can gain the most benefit from. Both interpretations are discussed below.

2.2.1. Phytocentric view

If we assume that selection acts mainly on individuals, it seems counterintuitive that plants would send carbon, nutrients or defence signals to their neighbours via a CMN. A possible explanation for this phenomenon is kin selection, whereby the donor can increase its 'inclusive fitness' (the fitness of its genepool including its family) by aiding in the survival of kin (Gorzelak *et al.*, 2015). Receiving signals about insect attacks can be greatly beneficial for the receiver plant because it can activate its defences in time and prevent damage by insect herbivory. There is evidence for kin selection in plants through aerial signalling via volatile organic compounds (Karban, Shiojiri, Ishizaki, Wetzel, and Evans 2013). Furthermore, there is evidence for kin selection between Douglas-fir seedlings through common mycorrhizal networks, where seedlings infused with radioactive C_{13} preferentially transferred it to close kin over unrelated plants of the same species in a greenhouse (Gorzelak., 2017). Gorzelak (2017) did not find that defence signals were transferred preferentially to kin as well, but given the evidence for CMN-mediated defence signal transfer between neighbouring plants (Song *et al.*, 2010; Babikova *et al.*, 2013a; Song *et al.*,2014; Song *et al.*, 2015), it seems plausible that kin selection can occur through these signals. Several other studies have also shown preferential C transfer to kin over strangers (Pickles *et al.*, 2017; Simard 2018), albeit through a soil solution instead of a CMN in the case of Pickles *et al.* (2017). Overall, it seems that the claim that plants can undergo kin selection through CMNs, at least in a greenhouse setting, is supported by evidence. Whether plants also preferentially send signals to close kin through CMNs remains to be demonstrated.

2.2.2. Mycocentric view

Some authors note that interpreting the limited evidence as kin selection means taking a phytocentric viewpoint. These authors (Babikova *et al.*, 2013b; Johnson and Gilbert., 2015) argue instead for a mycocentric viewpoint, where the fungus is in control of where resources and signals are sent. Mycorrhizal fungi depend on their plant hosts for most aspects of their functioning and survival (Smith and Read. 2008), so it makes sense that it would benefit the fungus to assist plants in

fending off insect attacks. There is evidence that fungi can choose a direction of nutrient flow and prioritize plants that supply more photosynthetic assimilates over plants that supply less (Kiers *et al.*, 2011). Based on this evidence and the observed interplant signal transduction through CMNs, Babikova *et al.* (2013b) outline four non-mutually exclusive hypothetical scenarios for how mycorrhizal fungi may benefit from different allocation of herbivore-induced signals to plants (figure 2):

A. Fungi preferentially allocate signals to plants that supply them with the most carbon.
B. Fungi preferentially allocate signals to plants that elicit the strongest defence response, such as the release of volatile organic compounds.
C. Fungi spread the allocation of signals to different plant phenotypes, such that in the event of a disaster at least one of these phenotypes is likely to survive.
D. Fungi preferentially allocate signals to plants that are primarily colonized by themselves and not also colonized by competing fungi.
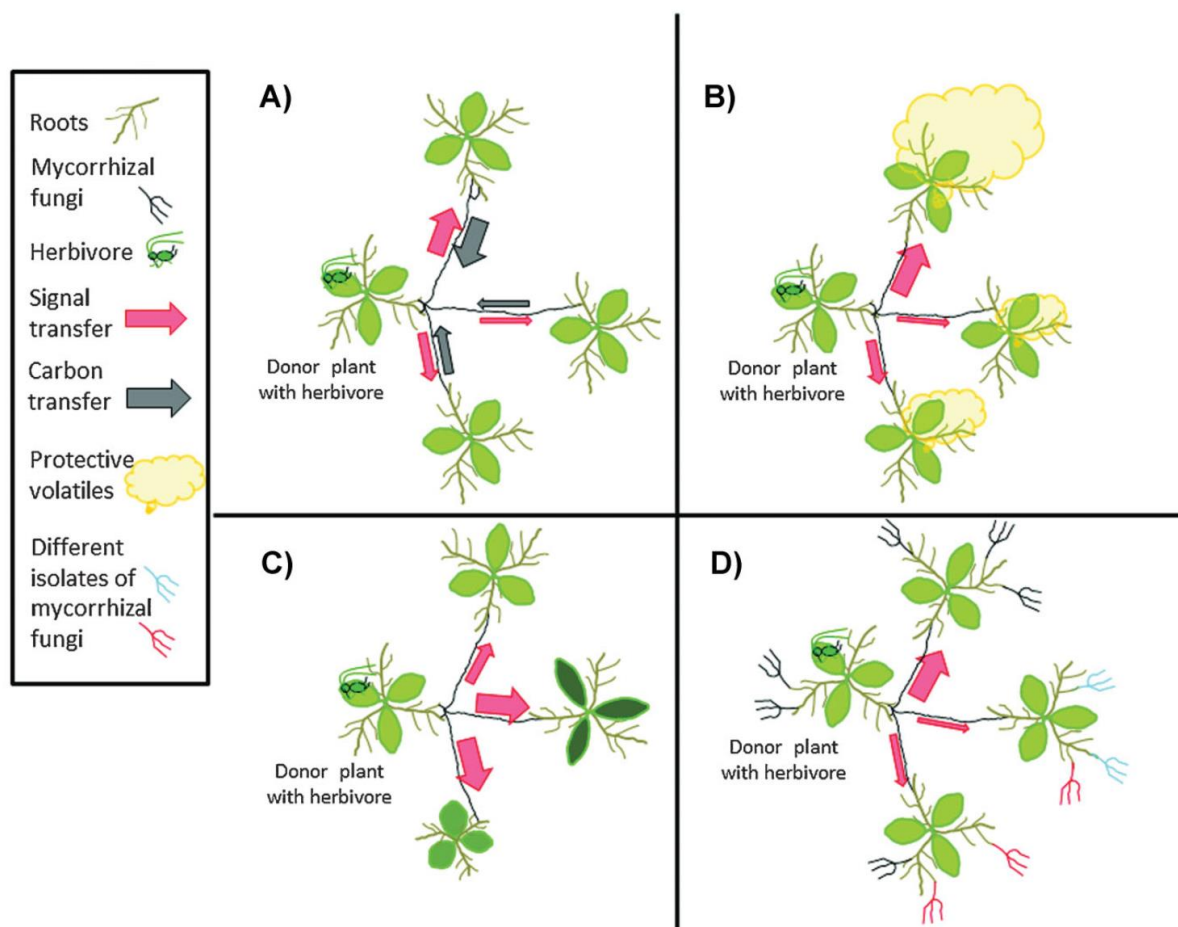
Figure 2: Hypothetical scenarios that outline reasons for fungi to send more signals to some plants and fewer signals to others. A) Fungi preferentially allocate signals to plants that supply them with the most carbon. B) Fungi preferentially allocate signals to plants that elicit the strongest defence response, such as the release of volatile organic compounds. C) Fungi spread the allocation of signals to different plant phenotypes, such that in the event of a disaster at least one of these phenotypes is likely to survive. D) Fungi preferentially allocate signals to plants that are primarily colonized by themselves and not also colonized by competing fungi (Babikova *et al.*, 2013b).

To my knowledge none of these hypotheses have yet been tested, and they will be difficult to test without first identifying the signal. A combination of multiple scenarios could also be the reason for fungi to control where signals are sent. It seems logical that fungi are at least partially in control of

the signal since it passes through them. There are substantial knowledge gaps in our understanding of fungal internal communication (Schmieder *et al.*, 2019), but it is known that fungi can move resources around themselves using microtubule "motors" at speeds faster than diffusion would allow. For example, some fungi can optimise the amount of photosynthate they receive from plants by actively hoarding, relocating and transferring nutrients to those plants that need them most (Whiteside *et al.*, 2019). Similarly, if the signal being sent between plants is chemical, microtubule "motors" could be used by the fungus to send the signal in a particular direction.

Fungi have the ability and reasons to control interplant signals sent through a CMN. I think that the mycocentric viewpoint is most likely to be true, given that fungi have been shown to be able to direct the flow of substances that pass through them. However, just like with the phytocentric viewpoint, it remains to be demonstrated that fungi exert this control.

2.3. Critical response to CMN ecological significance

Despite the large amount of research that has been done on CMNs since the discovery of Simard *et al.* (1997), many researchers are still not convinced that they play a major role in ecosystems. These researchers (Karst, 2022; Bever *et al.*, 2010) point to a lack of field studies showing CMN benefits to plants. Furthermore, studies that have been done to map CMNs in the field have used genetic markers to determine if plants are connected by the same individual fungus. However, there is no way to rule out that identical genetic markers do not belong to disconnected genets (individual fungal genotypes) whose hyphae were connected in the past but have now been severed by fungivory (Beiler *et al.,* 2010). If the latter were true, maps that appear to show connected CMNs may instead show disconnected fungal genets. Interestingly, mycorrhizal plants may be able to protect their fungal symbionts by sending protective chemicals into their hyphae. Duhamel *et al.* (2013) grew *Plantago lanceolata* with or without AM fungi, and in the presence or absence of fungivorous springtails. They found that the defensive metabolite catapol, which is known to occur in *P. lanceolata,* was consistently found in AM fungal hyphae when springtails were present. No catapol was found in hyphae when springtails were absent. These results suggest that plants can help protect CMNs from fungivory by providing fungi with protective chemicals, and this might contribute to the persistence of these networks over meaningful distances and timespans.

Several field studies have been performed that appear to show carbon and nutrients passing through CMNs between plants in nature (Simard *et al.*, 1997; Teste *et al.*, 2010), but according to Karst (2022) most of these studies either have methodological flaws or wrongly interpret the evidence as plants benefitting from a CMN. For example, Simard *et al.* (1997) likely underestimated the amount of carbon that was transferred through the soil in their study (Karst, 2022). Simard *et al.* (1997) compared carbon transfer by the AM *Thuja plicata* with carbon transfer by the EM *Betula papyrifera* and *Pseudotsuga menziesii*. They found that transfer of carbon isotopes to *T. plicata* averaged 18% of transfer between *B. papyrifera* and *P. menziesii*. However, AM fungi form less extensive mycelia than EM fungi, meaning that a nutrient is more likely to be absorbed by an EM fungus than by an AM fungus in an area where both occur (Karst, 2022). This suggests that the 18% finding by Simard *et al*. (1997) is likely an underestimate. Nutrients could also have gone through the soil at least part of the way instead of through a CMN exclusively. The same could be true for signalling molecules as well. In my opinion it is more likely that resources and signalling molecules move primarily through hyphae and not as much through soil. Hyphae can form relatively stable connections between plants, especially if plants help to protect hyphae from fungivory (Duhamel *et al.*, 2013). Competition in the soil is fierce between many types of arthropods, fungi and microbes. Signal and resources could get lost in soil more easily than in hyphae.

One of the studies that is often cited as evidence for interplant signalling through CMNs in field conditions is the one done by Song *et al*. (2015). At the time this study was published, only signal transfer through CMNs consisting of AM fungi had been investigated. Song *et al*. (2015) were the first to show that this kind of signal transfer could occur in lab conditions through EM fungi as well. They used pairs of seedlings consisting of a *P. menziesii* donor and a *Pinus ponderosa* receiver. The seedlings were subjected to one of three treatments: (1) grown together in a pot allowing for root and CMN contact (2) separated by a mesh with 35 µm pore size to allow CMN access but no roots (3) separated by a mesh with 5 µm pore size to keep out CMN and roots but allow diffusion through the soil. *P. menziesii* donors were then either manually defoliated or exposed to herbivory by western spruce budworm (*Choristoneura occidentalis*). Receiver plants produced defence enzymes in response to manual- and budworm defoliation of donor plants, which showed that signals could be sent between different plants through CMNs and soil diffusion (Song *et al*., 2015). Curiously however, this was only observed in treatments 2 and 3. There was almost no change in defence enzyme activity in receiver plants when they were connected to donor plants by both roots and mycorrhiza. Karst (2022) argues that this latter scenario is closest to conditions in nature because there is no such thing as a CMN in the absence of roots. The findings of Song *et al*. (2015) are therefore not evidence of interplant signal transfer through CMNs in nature. This strange result serves as a reminder that we should be careful when using lab studies as evidence for a phenomenon in nature. Above all else, it should motivate us to do more field studies to find out what the real effect of CMN mediated interplant signalling is in nature. But before these field studies are done, it will be helpful to first identify the signal that is passing through CMNs.

3. Comparing and testing hypotheses

Since the discoveries by Simard *et al*. (1997), many bold claims about the ecological significance of CMNs have been put forward. Several studies have been done that demonstrate carbon and nutrient flow between plants in nature, but no such studies have yet been carried out that show interplant signal transfer through CMNs. Until such studies are done, we can only speculate about the ecological significance of signal transfer through CMNs. In my opinion, the focus of future studies should be to identify the mechanism behind CMN-mediated interplant signal transfer. Once the mechanism is identified, field experiments to elucidate ecological significance should become easier since researchers will know what signals to look for.

Multiple studies have reported interplant signal transfer through CMNs in laboratories, but so far the identity of this signal remains unknown. Identifying the signal will be a crucial first step to eventually elucidate the significance of CMN interplant signalling in nature. As explained earlier, the signal might consist of multiple components (Rasheed *et al*., 2022). Within plants the jasmonate pathway is a likely mechanism for signal transfer (Song *et al*., 2014), but the fungal signal remains unknown. To identify the fungal signal (assuming it is chemical in nature), compounds will need to be extracted from hyphae that link multiple plants in a laboratory experiment. A protocol for extracting fungal secondary metabolites that could be used for this task was developed by Nickles *et al*. (2021). Alternatively, new methods for extracting substances from fungal hyphae would need to be developed. Compounds that are known to be used by fungi to influence plant physiology, such as chemicals that aid in mycorrhization, could be an initial focus (Boyno & Demir, 2022). Once various candidates have been identified, the signalling compound can be identified by genetically engineering strains of fungi that are unable to make one of the chemicals. If a signal is not transferred between donor and receiver plant when the synthesis of a given chemical is disabled in one of the strains, then it can be inferred that the disabled chemical is responsible for signal

transduction through the CMN. Once this chemical is identified, field studies can be done to trace movement of this chemical to determine CMN-mediated signal transfer between plants in nature.

Alternatively, the signal might be electrical in nature. The first and only experiment to demonstrate that electrical signals can pass between plants through a CMN is the one done by Thomas and Cooper (2022). However, they did not test for any response in the receiver plants other than the transduction of the electrical signal. Future studies should aim to combine the approaches of Thomas and Cooper (2022) and Song *et al*. (2015) to both test the transduction of electrical signals and the defence response in receiver plants. In a natural ecosystem, this could be tested by inducing a large electrical potential into a tree and measuring the surrounding trees to see which ones receive the signal (Thomas & Cooper, 2022). Before such studies could be done, it would first need to be shown that hyphae conduct electricity better than the surrounding soil.

There are many different views in the literature concerning the ecological relevance of CMNs. From no significance at all to sentient trees or ecosystems being one interconnected organism connected by the CMN. Much is still unknown about the functioning of CMNs, but determining the ecological significance of signals that pass through these "wood wide webs" will have to start by identifying what the signals are.

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