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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?

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Most land plants associate with mycorrhizal fungi that can connect roots of neighboring plants in common mycelial networks (CMNs). Recent evidence shows that CMNs transfer warning signals of pathogen and aphid attack between plants. However, we do not know how defence-related signaling via CMNs operates or how ubiquitous it is. Nor do we know what the ecological relevance and fitness consequences are, particularly from the perspective of the mycorrhizal fungus. Here, we focus on the potential fitness benefits for mycorrhizal fungi and outline hypothetical scenarios in which signal transfer via CMNs is modulated in order to acquire the most benefit for the fungus (i.e. acquisition of carbon) for minimal cost. We speculate that the signal may be quantitative and may elicit plant defence responses on different levels depending on the distance the signal is transferred. Finally, we discuss the possibility of practical applications of this phenomenon for crop protection.

Keywords:

■ arbuscular mycorrhizal fungi; common mycelial networks; defence-related metabolism; fitness consequences; herbivores; hyphae; rhizosphere signaling

Introduction

Most land plants associate with mycorrhizal fungi that provide them with

immobile nutrients and water from the soil in exchange for carbon used for hyphal growth [1]. During the initial stages of the symbiosis metabolic changes in the plants are necessary to achieve a

compatible interaction [2], for example altering plant defence hormones [3, 4]. As a consequence, mycorrhiza increase plant resistance against pathogens [5], nematodes [6], and abiotic stresses [1]. Mycorrhiza also induce changes in the emission of plant volatiles, making them more attractive to the natural enemies of herbivores, their predators [7], and parasitoids [8], thereby providing plants with additional protection.

A key feature of mycorrhizal fungi is their ability to form “common mycelial networks” (CMNs) where the hyphae of an individual can connect roots of the same, and different, plant species [9]. CMNs enable newly developed roots to become rapidly colonized by a fully functioning fungal mycelium, and are thus important for seedling establishment, plant competition, and diversity [10]. CMNs can also be formed by fusions of the same isolates originating from different plants [11]. Interestingly, recent work has shown that CMNs can transfer disease resistance signals from tomatoes (*Lycopersicon esculentum* Mill.) infested with leaf early blight (*Alternaria solani*) to uninfested neighboring plants [12]. The receiving uninfested tomatoes had increased disease resistance, increased levels of defence-related enzymes and expressed defence-related genes [12]. CMNs also transfer allelochemicals released by marigold (*Tagetes tenuifolia* Millsp.) in the rhizosphere that inhibit growth of

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Abbreviations:

CMN, common mycelial network; **AM fungi**, arbuscular mycorrhizal fungi.

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neighboring lettuce plants (*Lactuca sativa* L.), thereby having the potential to regulate plant community structure [13]. Furthermore, CMNs transfer signals released by broad bean plants (*Vicia faba* L.) infested with pea aphids (*Acyrtosiphon pisum*), eliciting emission of protective volatiles in uninfested neighboring plants, thus repelling aphids and attracting parasitoids (*Aphidius ervi*) [14]. CMNs thereby act as an early warning system against aphid attack [14] (Fig. 1). These three experiments used different species, different experimental designs, and different approaches to detect the transfer (molecular tools and disease scoring [12], chemical analysis, and plant growth bioassays [13], analysis of plant volatiles, and insect bioassays [14]). While the experiments of [13] and [14] used mycorrhizal plants that were either connected or unconnected to a “donor” plant via CMN, [12] also used a non-mycorrhizal treatment to also test the effect of mycorrhizal colonization on plant defence responses. These experiments complement each other and demonstrate that CMNs transfer a range of signals and chemical compounds between plants and trigger various responses in the receivers.

These findings mean that we must now revisit current paradigms of plant-to-plant communication, e.g. [15] to take into account the roles of root-associated fungal mycelia. It is important to consider the fitness consequences, not only for the plants receiving the signals, but for the mycorrhizal fungi sending the signals. Here, we discuss the major gaps in our current understanding of CMNs related to their role in plant signaling, and speculate about the potential fitness consequences to the fungi and regulation of defence-related signaling via CMNs. Finally, we consider the potential role of signaling via CMNs in crop protection strategies.

Ubiquity of CMNs in nature

While we know that CMNs can be formed in plant communities dominated by ericoid mycorrhizal [16, 17], ectomycorrhizal [18], and arbuscular mycorrhizal (AM) [19] fungi, we still have little knowledge about their extent and degree of connectivity. This limits our ability to gauge how important CMNs are for ecosystem functioning. We lack this knowledge primarily be-

cause the techniques used to investigate the distribution of CMNs in the field cannot adequately distinguish the connectedness of the hyphae. Therefore, most studies of CMNs are laboratory based where techniques such as autoradiography can be employed [9]. CMNs can be formed by one fungal isolate connecting two con-specific plants but may also involve several hetero-specific plants. Most plants are simultaneously colonized by several species or genotypes of mycorrhizal fungi [20, 21], and so a single plant might be involved in several functioning CMNs. Therefore, groups of CMNs can be indirectly connected via a shared plant, potentially extending the distance over which CMN-based signaling may occur (Fig. 1). The recent discoveries of defence-related signals between plants connected via CMNs [12, 14] were made using single species of AM fungi. We now need to determine whether other types of AM fungi are equally capable of transferring signals, and whether other mycorrhizal types can transfer signals, and over what distance.

What are the fitness consequences of defence-related signaling via CMNs?

Plants that receive a warning signal of aphid attack produce volatiles that repel aphids and attract parasitoids (that kill aphids) and so can clearly benefit from this signal. Signals from CMNs are likely to be of most importance between plants that are attacked by the same insect herbivore and that produce and detect the same volatiles, such as plants of the same family (e.g. the pea aphid and broad beans). However, what do AM fungi gain from transferring signals between plants? AM fungi rely on their plant hosts for carbon, essential for growth and most aspects of their functioning [1]. Aphids drain plants of carbon, severely damaging them [22], and can decrease mycorrhizal colonization of bean plants by 20% (Babikova et al. unpublished data). Therefore, it might benefit AM fungi to signal a warning to their host plants so that they can then repel or limit attack by aphids, thus maintaining carbon flow to the fungus.

Currently we do not know if the signaling between plants via CMN is

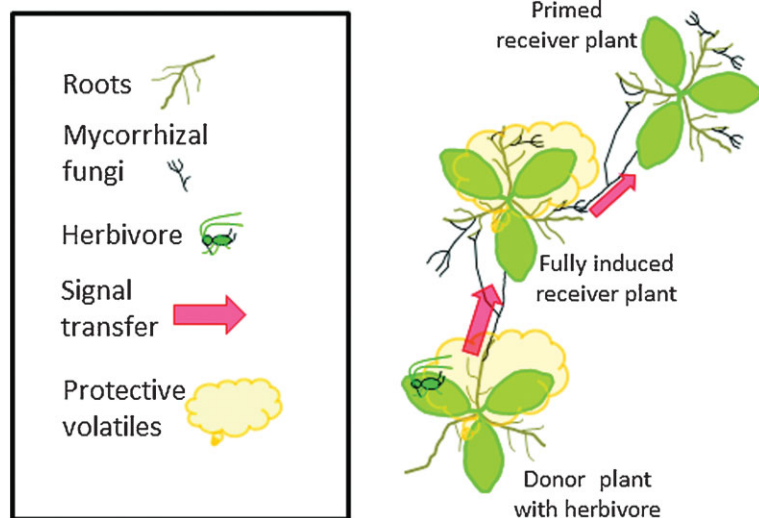


Figure 1. Defence-related communication between plants via a CMN. Herbivores induce systemic defence response in the infested plant leading to emission of protective volatiles that repel subsequent herbivores from the plant and also attract their natural enemies. A signal is transferred via the CMN to a neighboring plant to induce a similar defence response. We hypothesize that the signal might be transferred further to an indirectly interconnected second neighboring plant, and that it might “prime” that plant for potential future attack. Primed plants do not exhibit increased defence response; however, they respond more strongly and faster, if the attack occurs.

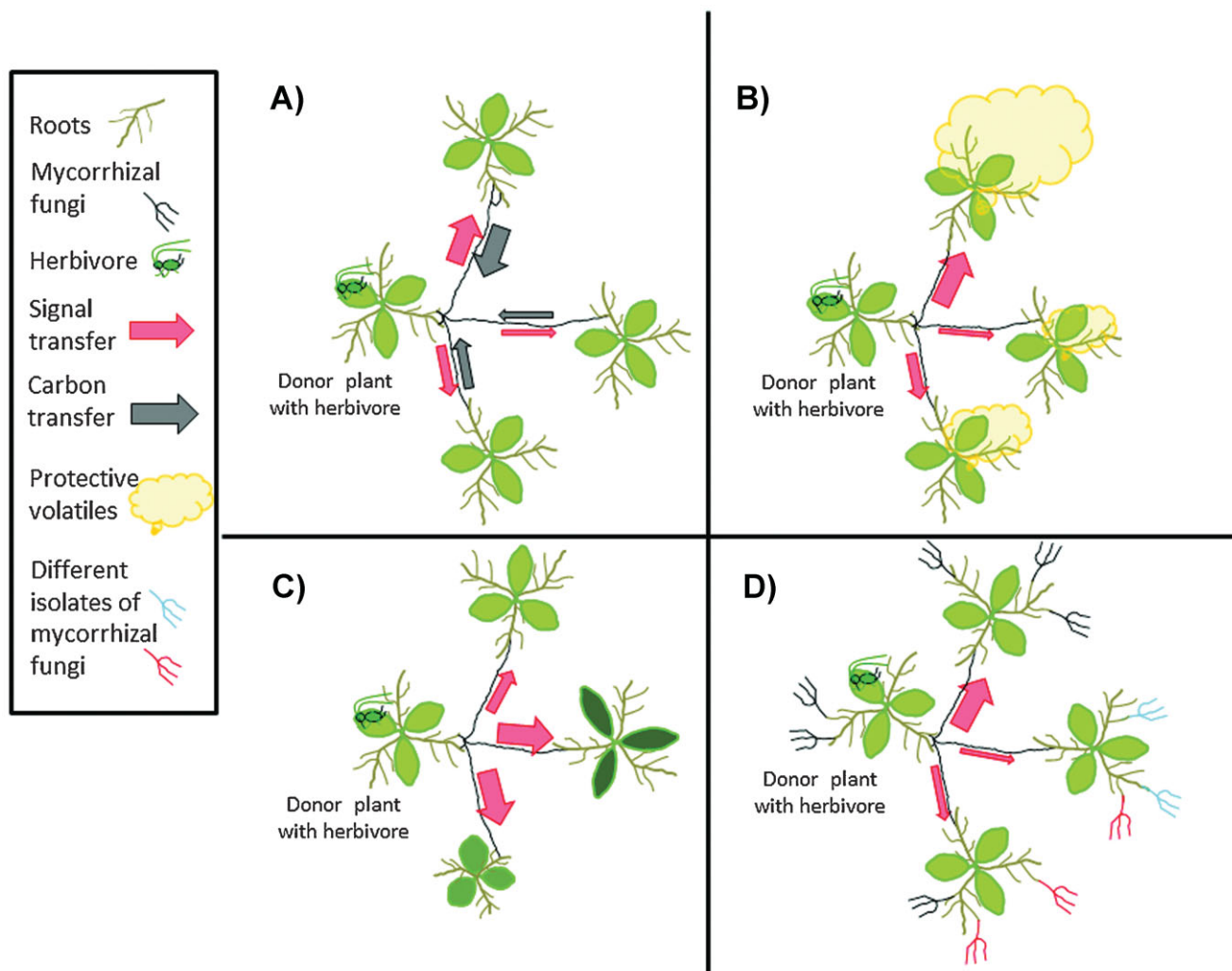


Figure 2. Hypothetical scenarios in which signal transfer via a CMN is modulated in order to acquire the most benefit for the fungus: **A:** The fungus preferentially allocates signals to plants that are of most immediate value to it in terms of the quantity of carbon that the fungus gains from the plants, thereby protecting its current most important carbon source. **B:** Signals are preferentially allocated to plants that elicit the strongest defence response, and hence are better at repelling herbivores and attracting the herbivore’s enemies via induced volatiles. **C:** CMNs are formed between different plant phenotypes so the fungus can “hedge its bets” against the scenario of loss of phenotypes; by warning a wide variety of phenotypes, there is a greater likelihood that one of them remains healthy, thereby maintaining carbon flow to the fungus. **D:** The fungus may withhold signals to plants that harbor extensive colonization by other competing fungi. If signaling is costly to the fungus, it might be predicted that the fungus gains greater benefit by signaling preferentially to a plant that is colonized mainly by itself, rather than to a plant that is colonized mainly by its competitors.

tially in phenotype, including in carbon allocation to the fungi and strength of response against herbivores. Therefore, if fungi can actively allocate signals, we might expect the fungi to partition the signal between host plants in ways that optimize their fitness, i.e. maximum benefit to the fungus for a given unit cost of signaling. Accordingly, here we outline four hypothetical, non-mutually exclusive, scenarios for how mycorrhizal fungi may benefit from differential allocation of resources (in this case herbivore-induced signals) to plants (Fig. 2A–D).

In the first hypothetical scenario (Fig. 2A), we speculate that the fungi preferentially allocate signals to plants that are of most immediate value to them in terms of the quantity of carbon the fungus gains from the plants. In doing so, these plants can respond quickly against aphid attack [24] so the fungus’ most important carbon

active or passive or whether it is the plants or the fungi that control the signals. CMNs provide physical conduits for surface water flow, which could facilitate the passive movement of root exudates’ components. Accordingly, in the past it was presumed that the transfer of nutrients and water between plants via CMN is passive and follows a source-sink gradient [9]. However, there

is now evidence that AM fungi can choose a particular destination for delivery of nutrients to plants [20, 23], preferentially allocating resources to those roots that supply the most assimilates [23]. We speculate that this might provide a mechanism via which defence-related signals could also be allocated to particular plants. Plants connected to CMNs may differ substan-

source, essential for their growth and survival, is protected. This hypothesis could be tested by quantifying carbon allocation to mycorrhizal fungi [25–27] and measuring the strength of the signal transmitted through the CMN. However, so far we do not know what the signal is, nor how to measure it directly. A rough proxy could be to measure the change in plant volatiles or the change in attractiveness of plants to aphids. Additional refinements may be required including quantification of the extent of fungal colonization, because it is reasonable to expect signal transfer (and plant allocation of carbon) to be partially dependent on this parameter.

In the second hypothetical scenario (Fig. 2B), the signals are preferentially allocated to plants that elicit the strongest defence response, thereby better repelling herbivores and attracting the herbivore's enemies by the plant's induced volatiles. This carbon source (even if it is not the greatest carbon source) is therefore well protected. Furthermore, neighboring plants may detect the aerial volatiles produced by this strongly-reacting receiver plant, and respond by launching their own anti-herbivore responses [15], at no extra signaling cost to the fungi. The fungus then gains direct and indirect protection of several of its carbon sources by preferentially allocating signal to the plant that produces the greatest volatile response.

In the third scenario (Fig. 2C), we speculate that the fungus can spread the allocation of signals between diverse plant phenotypes (this could occur between species, within species or even within genotypes) in order to “hedge its bets” [28]; the opposite of “putting all your eggs in one basket”. In this way the fungus helps protect a variety of phenotypes, such that at least one or a few might survive in the event of an adverse situation such as a disease outbreak or drought. This “strategy” would reduce the risk to the fungus of losing all its carbon sources in the long term. Such a situation might occur particularly in more unpredictable or unstable environments.

The fourth scenario (Fig. 2D) considers signaling via CMNs in the context of competition between fungi, since different mycorrhizal fungi compete for space on plant roots. Trees can

withdraw support to mycorrhizal fungi that provide nutrients to competing trees [29] so, if the reverse can also occur, we speculate that fungi may withhold signals to plants that provide carbon to other competing fungi by virtue of being colonized by them. Thus, the fungus may benefit by signaling preferentially to plants colonized mainly by itself, rather than to plants colonized mainly by competing fungi. This scenario assumes that plants are incapable of allocating carbon to particular fungi on their root systems. This seems to be partly supported because differential allocation of carbon to AM fungi at very fine scales (within a segment of root) does not seem possible, although allocation to AM fungi on larger scales (different sections of root) can occur [20].

The benefits to the fungi of transferring defence signals via CMNs may also feed back to positively affect infested donor plants, for example, through maintaining mineral nutrient uptake via the mycorrhizal mycelium. Several potential benefits to plants of initiating signal release (via aerial pathways) have been discussed [15]; the role of signal transfer via CMNs may thus provide a further explanation.

How is defence-related signaling via CMN regulated?

Plants have evolved mechanisms to perceive information about their environment, neighboring plants, and other organisms using chemicals in root exudates [30] and volatiles [31]. Perennials grow next to their neighboring plants for many years and each year these plants can become attacked by various herbivores and pathogens. Defence-related communication between these plants could hence be repeated or perhaps even continuous. Therefore, it seems possible that CMNs may elicit plant defence responses at different “levels”, from very little, up to full induction. In previous studies [12, 14], the defence responses of receiver plants were fully induced, i.e. the composition of volatiles released changed [14], defence-related genes were expressed and defence-related enzyme activity increased [12]. However, this incurs a

high metabolic cost to the plants [32] and may be worthwhile only if the attack is underway or imminent. In the experiments of [12, 14], the plants were grown relatively close to each other (15 and 20 cm, respectively) but we do not know the distance over which defence-related signaling via CMNs operates, or whether the effect decreases with distance along the CMN. Perhaps full induction of plant defences occurs over only short CMN signal distances, while more distant plants may be only “primed” (Fig. 1), which is less expensive to the plant than full induction, and enables the plant to respond to attack faster and more strongly once it takes place [33].

Aboveground communication between plants via airborne volatiles can occur between different plant species [15] to a distance of approximately 60 cm [34]; however we do not know how common aerial communication is in nature. It has been suggested that systemic resistance to herbivory results from signal transfer via a combination of aerial and vascular pathways [32]. We now need to test the importance of signaling via CMNs relative to airborne volatiles, and how aerial, vascular, and CMN signaling interact to affect overall resistance to herbivory.

Can defence-related signaling via CMN be applied to protect crops from pests?

There is an intriguing question that emerges from the recent findings that plants can warn each other about herbivore attack using CMNs: might this phenomenon be exploitable in crop protection strategies? For example, it may be possible to grow susceptible “sentinel” plants which are the first plants to be attacked by the insect pest, thereby warning the rest of the crop via the CMN. Simply reducing tillage could encourage formation of CMNs, thereby allowing rapid pest-induced responses by the crop. Alternatively, identifying the CMN-based signal and finding new chemical elicitors of systemic resistance might provide more efficient and targeted crop protection regimes. This

might be important if the metabolic cost of induced defence leads to decreased crop yields [35].

Yet caution should be applied in this respect, because the mechanism of the signaling through the CMN is currently only theoretical [36]. Because defence-related systemic signaling via plant vascular tissues differs between plant-herbivore species combinations [32] the chemical mechanism may also differ between species of plants and fungi. Intriguingly, there is also a possibility that the signal is not chemical but electrical. Herbivore-induced early defence response in plants involves cytosolic Ca^{2+} spiking, leading to changes in electrical potential on the surface of the cell followed by an electrical signal (action potential) [37]. The speed of this electrical signal is much faster (40 m/s) than transfer of chemical signals via vascular tissues [38], and the signal travels through the entire plant from the point of perceived input [37]. The electrical signals activate biosynthesis of jasmonate in distal leaves and the genes involved in transmission of these signals were recently identified in *Arabidopsis* [39]. If the electrical signal reaches sites of mycorrhizal colonization, and if it can continue beyond via the CMN, then this could potentially lead to the development of novel electrical crop protection treatments.

Conclusions and prospects

So far, research on the mutualistic relationship between mycorrhizal plants and fungi, including CMNs, has largely focused on reciprocal exchange of carbon, nitrogen, and phosphorus between partners. We now know that CMNs formed by AM fungi also function as avenues of defence-related signals between plants [12–14], raising the need to consider the fitness consequences for fungi, plants, and insect herbivores. Reciprocal transfer of resources between partners is likely to remain a key process underpinning the mycorrhizal symbiosis. However, a greater emphasis can now be placed on the ecological and evolutionary importance of signal transfer, and the question of whether this process leads to trade-offs in resource allocation between partners.

From an applied perspective, furthering our understanding of the full complement of mycorrhizal functions, including their roles in plant defence, may enhance food security.

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