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Interplant communication

The role of mycorrhizal networks concerning underground interactions

Sous la direction de **Séraphine Grellier** **Nina Boutafa**

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The role of mycorrhizal networks concerning underground interactions

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Le travail de recherche, dont l'objectif de base est d'acquérir une compétence méthodologique en matière de recherche, doit répondre à l'un des deux grands objectifs :

- Développer toute ou partie d'une méthode ou d'un outil nouveau permettant le traitement innovant d'un problème d'aménagement
- Approfondir les connaissances de base pour mieux affronter une question complexe en matière d'aménagement.

Afin de valoriser ce travail de recherche nous avons décidé de mettre en ligne sur la base du Système Universitaire de Documentation (SUDOC), les mémoires à partir de la mention bien.

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USEFUL ABBREVIATIONS

CMN: Common Mycorrhizal Network

MF: Mycorrhizal Fungus

AMF: Arbuscular Mycorrhizal Fungus

EMF: Ecto Mycorrhizal Fungus

MH: Myco-Heterotrophic

VOC: Volatile Organic Compound

Interplant communication: The role of mycorrhizal networks concerning underground interactions

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ABSTRACT

Aerial and belowground interplant communication have been recently drawing attention within the scientific community over the four past decades. Hence, most of studies agree to confirm that interplant communication is relying on effective cross talks of molecular substances between at least, one emitter and one receiver. The discovery of mycorrhizal symbiosis since 1885 between fungi and plants and thereby, the formation of interspecific common mycorrhizal networks around the 80's, was a significant step for the below ground interactions study. Nowadays, it is suggested that soil communication through hyphal pathways represents a key component for enhancing fitness and competitive advantage of networked members. This bibliographic synthesis is giving an overview of the tremendous role played by mycorrhizal fungi and the wide effects of such communication. It also highlights some study fields which need to be pursued to clarify plant-fungi belowground interactions.

INTRODUCTION

During the 1980's, the first proofs of interplant communication have been recorded in literature. The most famous event which made scientific researches started, is the discovery of 3000 dead koudous in South Africa due to an impressive defensive mechanism of acacia trees in this region (mentioned in Daugey, 2018). Rapidly, it provoked an increasing interest among the scientific community concerning interplant interactions and its integration within human technology. Communication among plant remains a very recent study area which presents many unexplained observations. To illustrate, even the definition of communication is still debated. Indeed, there is a lack of precise and unanimous definition. Barto and her co-authors (2012) are giving an overall and neutral definition which can be applied to every discovery in the field: "*Communication is driven by the exchange of substances released by one organism and detected by another*". But in the same time, Maynard Smith and Harper (2003) and Scott-Philips (2008) are claiming that communication, to occur, needs to be both beneficial to either the receiver and the emitter. The opposite definition has been also presented, explaining that senders and recipients are not expected to get benefits from communicating processes (Karban, 2008; Barto et al., 2012). In this scientific review, the latter definition has been kept for dealing with communicating mechanisms. Related to it, another debate concerning the adequate term to designate exchanged substances has been also presented. First, the term of "signal" could potentially be found within the literature. According to Van't Padje et al (2016), the word "signal" is used when sender and emitter, both gain a fitness advantage for communicating. For instance, microbes and plants are sending signals to each other to indicate their colonization readiness. Second, "cues" could also be employed to designate a one way benefit to receivers only (Van't Padje et al., 2016). Yet, cues and signals are not perfectly delineated. In the following parts, the most accurate term would be "infochemicals" which integrates "*all the substances [...] used in communication*" (Barto et al., 2012). Communication isn't only dealing about intraspecific relations but can also occur within interspecific communities. Plants can actually communicate with surrounding plants, animals, microbes, fungi and insects (Barto, 2012). Nowadays, two different ways of interplant communication have been highlighted. The most well-known type is the airborne communication. This aerial system has many roles such as providing an efficient signaling and defense system among plant population or attracting pollinating insects by relaying perfumes and hormones (Daugey, 2018). The second type is dealing with underground plant and soil fauna interactions. Indeed, it has been proven that plants are emitting infochemicals through the soil matrix via root exudates (Bais et al., 2004; Barto et al., 2012; Gorzelak et al., 2015). Communication is occurring when enough concentration of those substances can get through soil barriers to attain other organisms and then invoke a physiological reaction (answer) from receivers (Barto et al., 2012). But these exudate chemicals have a much reduced scope and can be conveyed only for decimeters from their source (Bais et al., 2004). However, this limited phenomenon was, interestingly, sufficient to mycorrhizal formations between plants and fungus (symbiosis). Mycorrhiza firstly discovered in 1885 by the German botanist Albert Franck, represents a good example of a successful underground communication process. Later, in the 80's, studies started to demonstrate the presence of belowground Common Mycorrhizal Networks (CMNs) (Wilkinson, 1998) which roughly are hyphal connections linking roots of neighbouring plants together. Mycorrhizal pathways are belowground networks which appear to be essential for interplant communication.

Hence, the final goals of this scientific review is to understand:

- What role may play Mycorrhizal Fungus (MF) through the establishment of CMNs in interplant communication processes?
- What are the main effects of belowground hyphal communication?

To obtain an accurate and complete answer to these questions, this paper is based on around 40 references (scientific articles and books) from the 70s to nowadays (most of them concern the 10 last year's period) and is structured in three main parts. Firstly, it is about compiling the scientific knowledge about CMNs and its functioning from an ecological and biochemical perspective. The second part is giving clues about the reasons why mycorrhizal fungus would permit soil fauna and flora communication. Thirdly, recent findings about underground communication effects via MNs are explored.

I. COMMON MYCORRHIZAL NETWORKS WIDELY USED FOR UNDERGROUND COMMUNICATION

1. Presentation

It's already admitted since more than a century, (135 years) that most of vascular plants (around 70%) are living in symbiosis with Mycorrhizal Fungus (mentioned in Van't Padje et al., 2016). A mycorrhiza is a symbiotic association between a fungus and plant roots. In this mutualistic relationship, a plant exchanges derived carbon from photosynthesis, called luxury goods (Walder et al., 2012), with fungal foraged soil nutrients including Phosphorus or Nitrogen (Gorzelak et al., 2015). These mineral elements represent scarce resources for plants which cannot fix it in the soil. Thanks to mycorrhiza, 90% of plant mineral requirements are filled up (Walder et al., 2012). In the other side, the fungus is a heterotrophic organism and hence, cannot live without this constant plant carbon input. That's why each organism is taking advantage of these transfers of resources and neither is harmed. Both parts had evolved during 450 MYA to be able to do it (Van't Padje., 2016).

MF can connect roots of neighbouring plants together and build up an entire belowground network called Common Mycorrhizal Network. Individuals of the same or different species may be found in such networks of both fungus and plants (Simard and Durall, 2004). CMNs can contain hundred to thousands of organisms (plants, bacterias, fungi) and even the number of individuals involved remain confuse to experts (Simard et al., 2015).

Currently, it is admitted that fungi can be classified as host-generalists or as host specifics. In most cases, fungi are host generalists: they can associate themselves with multiple plant species. Only a single individual could be enough to form a CMN. There are also possibilities of such CMNs to fuse together through hyphal connections. This fact has been proven thanks to a tracing nutrient experiment of host plants in their merged CMNs (Walder et al., 2012).

In the other hand, few fungi are specialists. In this case, mycorrhizal symbiosis occurs only within a group of individuals from the same specie. Gorzelak and her co writters (2015) are also talking about inclusive and exclusive MNs. They are not seeing the network from the fungal perspective (as done above) but from the plant vision. An exclusive MN is when a group of plants had mycorrhizas with the same fungal specie. A network which links diverse species of both fungus and plants is designated as inclusive and it's commonly the case in belowground interactions.

We can distinguish two main types of MF. The most ubiquitous one is named Arbuscular Mycorrhizal Fungus (AMF). The second one is the Ecto Mycorrhizal Fungus (EMF) which can be found in boreal, temperate and tropical forests. Indeed, EMF can be linked with most of the woody shrubs, coniferous tress and the Dipterocarpaceae living in those ecosystems (Gorzelak et al., 2015).

The majority of AMF and EMF species are host generalists. And due to their lack of host specificity, MNs are extremely species diversified. It has been recently demonstrated that infochemicals can be transferred through both AMF and EMF pathways (thanks to fluorescent dye experiments from Barto et al., 2012).

Barto et al., (2012) are also suggesting that fungi is caring to maintain a high connectivity within the network. In fact, they are taking carbon from their hosts and it is extremely advantaging for their own survival to ensure a long life time to each carbon supplier.

However, other experiments focused on parasites within mycelial networks and discovered that myco-heterotrophic plants (parasites) can join CMNs to both benefit from nutrient and carbon transfers (Bidartondo et al., 2002; Courty et al., 2011).

These nutrient transfers highlight the importance of belowground networks which allow plant coexistence and communication in diverse ecosystems. Thanks to these discoveries, CMNs recently begun to be considered as a major actor of communication transfers offering direct connections from supplier to targeted plant. As already discussed in the introduction part, plants do have a bioactive zone to convey infochemicals toward other organisms though the soil matrix but many biotic and abiotic barriers stop the diffusion of those elements. According to the Network Enhanced Bioactive Zone model, mycorrhiza are extending this bioactive zone (figure 1) by facilitating infochemicals mobility (especially allelopathic ones) and thus, can be seen as "superhighways" (Barto et al., 2012).

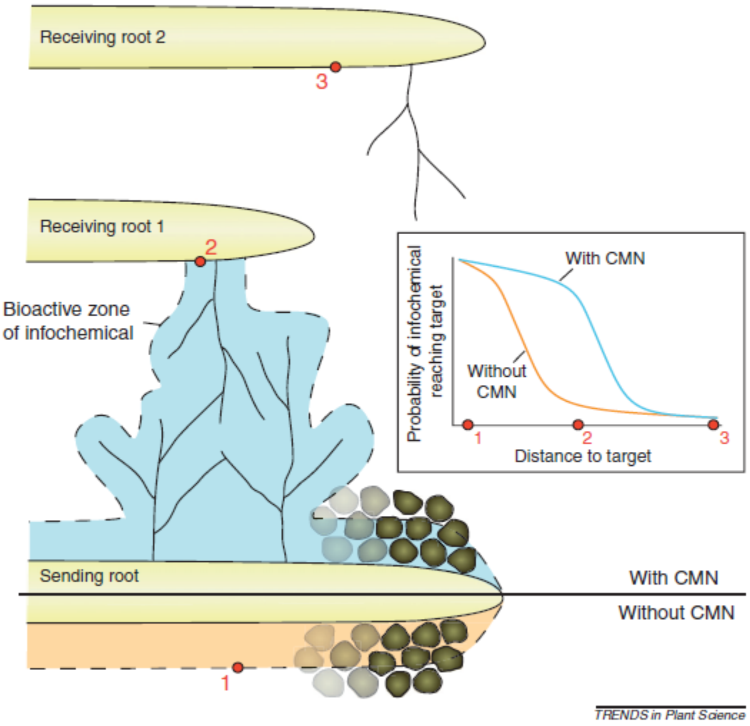

Figure 1: Enhanced bioactive zone of allelochemicals thanks to CMNs (Barto and al., 2012)

In this case, hyphal pathways offer a competitive advantage to overcome these disruptions for networked plants over non networked organisms. Thus, mycorrhizal structures provide safer and faster passages for the exchange of compounds (Simard et al., 2015).

Walder and his co-authors (2012) propose to imagine CMN as a "market place" where fungus and plants are constantly trading luxury goods and limited resources. In the same time, Gorzelak et al., (2015) are talking about a complex adaptive social system (related to the Complex Adaptive System theory) into which plants and fungi are interacting, sending information feedbacks and constantly adapting to environmental shifts. Simard et al, (2015) are completing by affirming that these cross scale flows are leading to the self-organization of the network. They believe that this huge global system is a grouping of many local and overlapping networks. A local change of functioning or properties may affect and propagate into the whole system.

2. Communicating through fungal pathways, process and functioning

It has been demonstrated above that plant-plant and plant-fungi communication constantly occur into the rhizosphere thanks to mycorrhizal connections. In this part, we focus on the practical aspects of these message transmissions. The followings are the main questions we tried to answer here. What kind of molecules are conveying? How are they transported to the targeted organism?

Different kinds of molecular exchanges

Since 30 years, experiments have revealed several different messaging compounds transmitted via CMNs. Plants and fungi are dealing nutrients, defence and stress signals, allelopathic chemicals, plant hormones, water and even genetic material (Giovannetti et al. 2004) and metals (Meding and Zasoski, 2008).

First of all, organic molecules including water, nutrients and lipids are known to be transmitted via hyphal connections. Concerning nutrients, nitrogen, phosphorus and carbon have been shown to flow between members of the community. Some nutrients are sometimes associated together to be transferred. It is the case for nitrogen and carbon which appear to be transported together as a simple amino acid form inside mycelial connections (Simard et al., 2015). Water transfers have also been studied: nowadays, it is known that these fluxes are bi directional and have a diurnally functioning (Barto et al., 2012). Depending on the type of Mycorrhizal Fungus involved in the network, AMF or EMF plants are not sending the same kinds of molecules. For example, Bago et al, (2002) demonstrated triacylglycerol (lipid) flows within only AMF mycelia. In the other hand, in EMF networks, Simard et al, (2015) succeeded to quantify the percentage rate of plants that fulfil their organic compounds requirements thanks to hyphal nutrients exchanges. They found that most of Myco-Heterotrophic (MH) plants linked to the CMNs benefit from carbon fluxes (85% for partial MH organisms and 100% for normal MH individuals). This fact explain how heteroptrophic plants could survive in CMNs without supplying carbon but, in fact, receiving it (it is essential for their own subsistence). As parasites, myco-hetrotrophs are profiting from resources without paying the CMN joining cost in return. Concerning autotrophic organisms, the rate is fluctuated around 0 to 10%. Dealing with the nitrogen, 40% of N needs of non N2 fixing plants have been supplied. These rates can fluctuate in function of the king of MF involved.

Du to this tremendous network, plants have the possibilities of sending allelopathic molecules through hyphal mycelia (Barto et al., 2011). Allelopathy represents all the chemical interactions between soil organisms and plants. Rice (1974) described it as all damaging consequences (in a direct or indirect way) provoked by the transfer of allelochemicals into the environment and orchestrated by one plant toward others. It plays a big role concerning interspecific cooperation, competition for environmental resources (like light or water) and defence processes against predators. For instance, it means that individual can inhibit the growth of other plant organisms and even microbes and bigger soil animals. Natural inhibitors as thiophene, and herbicides like imazamox (Gorzelak et al., 2015) can be quoted. An experiment has been driven in lab to assess the sensibility of tomato plants to allelochemicals when connected to CMNs. And the results are proving that tomato plant is receiving juglone, another inhibitor that most of agricultural and ornamental plant species are sensitive to (Crist and

Sherf, 1973). In this case, it provokes a reduced development of plants. And paradoxically, control tomato plants were bigger when unrelated to CMNs (Achatz and Rillig. 2014). Usually, a big concentration of infochemicals is needed to get through the rhizosphere barriers to be ecologically efficient. Indeed, allelochemicals are particularly affected by soil moisture, microbial communities and organic compounds. But thanks to hyphal pathways, transfers of these molecules have been considerably simplified (which results in an extended bio active zone of allelochemicals). To confirm this fact, it has been observed that soil containing CMNs are displaying a higher concentration of inhibitors than in soils without hyphal connections (Barto et al., 2011).

Hyphal interactions do not only include allelochemicals but also hormones and defence signals. Indeed, Babikova et al, (2013) focused on belowground warning cues related to aphid attacks and they noticed that presence or absence of a CMN was determinant in defensive responses of neighbouring plants connected to aphid infested individuals. Even if airborne defence signalling processes remain widely used by the vegetal community, underground messages also appear to be essential. And MF seems to be a key agent for transferring these messages. As well as aerial signalling, underground pathways are able to transmit Volatile Organic Compounds (VOCs) which are emitted systemically by injured plants (Chamberlain et al. 2001). They demonstrated that surrounding aphid free plants when receiving these VOCs via CMNs, were activating defence metabolism such as the harmed plant did. Besides, the concentration of VOCs in headspace samples was higher from plants linked with aphid infested sender than from non-aphid infested organisms. In this experiment, the main inducing defence driver agent was methyl salicylate. This molecule when released in the atmosphere and rhizosphere, can attract parasitoid and repel multiple species of pea aphid (among many other defensive roles) according to Hardie et al, (1994).

Another signal molecule unrelated to defence processes, has been identified: Strigolactone can be found in AMF networks and are emitted by connected plants. Its effects are multiple but it's possible to quote an enhanced attraction of AMF around plants and the activation of the fungus metabolism in favour of plant growth. Strigolactone is also known to surprisingly attract parasitic plants (including Myco-Heteroptrophs). The latter are using it as cues (for their own benefit). Strigolactone represents a major signal compound in interplant communication (Van't Padje et al., 2016).

Informations about the characterization of transferred molecules seem to be very diffuse and uncomplete. More experiments are needed to obtain an accurate listing of all the possible compounds which can be conveyed through CMNs.

Transport of infochemicals through mycorrhizal networks.

We previously focused on the multiple kinds of exchanged compounds through hyphal pathways. But how are CMNs structured? Are there different possibilities for infochemicals to be transported from one organism to another?

Indeed, CMNs present a complex and highly optimized structure (figure 2) where infochemicals could flow via 5 different ways (Barto et al., 2012). The first one is the cytoplasmic area (symplatically) (1). In fact, organic compounds need membrane transporters to cross hyphal walls and current experiments are still trying to identify and demonstrate the presence of such transporters. Even if symplatic passages remain to be confirmed in CMNs, there is a high probability for infochemicals to use it. For the second way of transportation, hypotheses are made saying that non polar organic compounds could possibly be conveyed apoplastically (within the cell wall) (2). Indeed, this membrane is constituted of hydrophobic elements and represents a strong barrier to the passage of water fluxes containing nutrients and other molecules (Barto et al., 2012). Simard et al, (2015) state that carbon and nutrients are going toward the targeted organism by these two pathways (symplatically and apoplatically). Thirdly, water is flowing on the surface of the hyphae (3), and hydrophilic infochemicals (for example, allelopathic compounds like thiophene according to Barto et al, 2011) could easily be carried by these water fluxes. Those three ways can be taken simultaneously by chemicals (Barto et al, 2011). Another possibility is about the hyphal cord (4) formed when several hyphae kink together. The interior of the cord can be appropriate for the passage of water or air which can respectively contain water soluble substances and VOCs. In the other hand, this association of hyphae (cord) remain very rare in comparison of the probability of occurrence of a single hyphal structure. This path doesn't represent the main route which can be taken by organic compounds. To finish, the last way is concerning the hydrosphere (5). The presence of hyphae may modify the abiotic conditions of soil (such as conductivity and the aggregation of matters). Therefore, these phenomena may accelerate the movement of infochemicals contained into the water part of soil around CMNs. The other paths (except the surficial one) quoted before, remained more efficient because they avoid soil disruptions and offer a faster transfer thanks to less tortuosity of the hyphal structure (Barto et al., 2012).

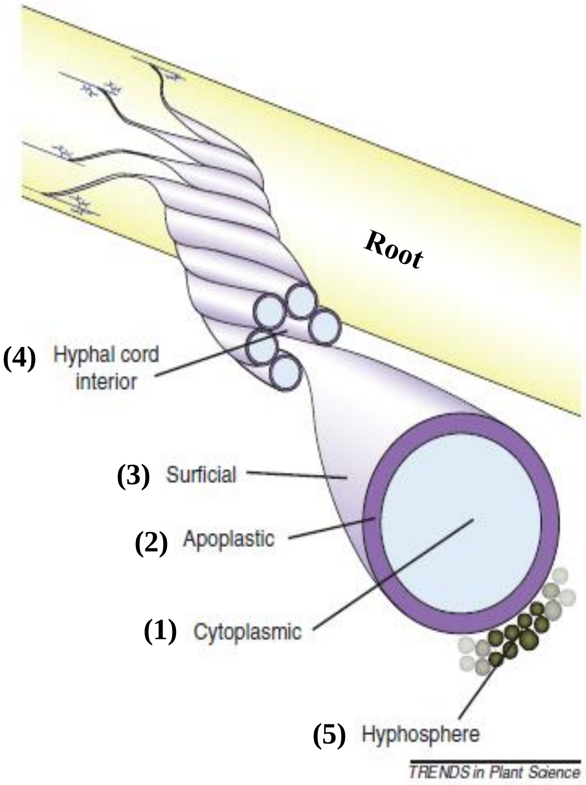

Figure 2 : Structure of CMNs and possible routes for infochemical fluxes (Barto et al., 2012), modified by N. Boutafa

Additional experiments are required to get more rigorous datas regarding polarity and size restriction of transported molecules. There are also several studies to be done for clearly determine which pathways are the most likely to be used by infochemicals (Barto et al, 2012).

A source sink relationship

Transfer of organic compounds is driven by a source sink relationship shared by all the members of the CMN: a nutrient/carbon enriched organism (source) will act as a donor with a plant into the vicinity which appears to be poor of these elements (sink or receiver). The nature (importance, quantity and frequency) of transfers based on source sink relations are depending on several located conditions. According to Simard and her co-authors (2015), factors influencing the nature of transfers are the excess luxury good status of the donor and the receiver plant, the nutrient quantity in soil, the mycorrhizal dependence of plants and the kind of fungal species within CMN. These facts have been confirmed notably though an experiment realised by Gorzelak et al, (2015) dealing with the allocation of resources in Douglas fir community. They demonstrated that adult Douglas fir individuals were able to transmit their nutrient surplus (carbon and nitrogen) to young seedlings in need. But this source sink relationship doesn't only occur in an interspecific way. In fact, it was also shown that Douglas fir trees can send mineral elements to paper birch. The latter would gradually return back nutrients in a different time period when its survival situation can allow such costs (Philip, 2006; Simard et al. 1997b). Studies are suggesting that, first, the donor may give nutrients or photosynthate carbon in excess to the networking fungi. These elements are, then, delivered to receiver plants in function of the strength of the source sink relation (Teste et al. 2009). Here, the fungi can be seen as a resource supervisor which receives vital elements for plants from donors and put it on hyphal pathways. Based on a source sink relationship, belowground communication mechanisms no longer appear to be related to a voluntary intention of the plant to communicate. Hence, the term, itself of communication remain a source of debate. In the other side, Gorzelak and al, (2015) are dealing with a possible control of the donor plant concerning the luxury good quantities it is able to exchange.

The degree of infochemical transfer control within plants and fungi

In both EMF and AMF networks, studies have reported proofs concerning behavioural nutrient transfer control of both fungus and plants. Indeed, generous carbon transfers from plants to networked fungus are rewarded, in the same way, by more fungal phosphorus fluxes toward the plant. CMNs seem to be structured on the basis of bidirectional control of sent resources by both entities. thus, some plant-fungal couples seem to be more advantaged than others by rewarding each other. This kind of relation is greatly favourishing cooperation and stability of the symbiosis. Besides, this may also involve bidirectional influence between plant and fungus (Simard et al., 2015). In fact, plant could be able to moderate the fungal phosphorus adsorption in function of its needs. In the other hand, fungus can choose to accumulate a higher quantity of Phosphorus when connected to little advantaging plants and then manages by itself the amount of scarce resources it wants to deliver to hosts. Networked organisms seem to have the possibility of deciding the magnitude of transfers and choosing the recipient to favour or not. In the same time, if a fungus retains the Phosphorus flow toward a specific plant, the latter can easily cut photosynthesis derived carbon exchanges off. It would directly affect the capacity of the fungus for colonization. For avoiding plant abuses (see part III), fungus could also handle carbon and nutrient supplies to, first, fill up its own needs and then encourage “good” plant behaviours which reciprocate in kind. This plant-fungus control over resources steadies the food input in CMNs. Studies are highlighting a great evolutionary advantage for networked organisms (Simard et al., 2015).

The entrance in CMNs has been previously presented as a compulsory, equal and fair nutrient payment of each part of the community. Here, modalities of transfer no longer appear as standardized but quite more nuanced and complex with different plant-fungus strategies to get more nutrients for their own.

Further explanations are required to fully understand mechanisms which induced plants to communicate together. Is it only due to a source-sink relationship which refers to an involuntary and physiological reaction? Or are plants really choosing and controlling what they are sending to others?

The scope of infochemicals

Many experiments are trying to measure the length of MNs and thus, determining the time which is needed for information to attain the targeted organism. As previously indicated, CMNs are scale free (Gorzelak et al, 2015). Hyphal pathways can extend from at least, tens meters to hundreds of hectare under forests for example (Beiler et al. 2010). Barto and her co-authors affirm that the length of AMF belowground networks are enhancing thanks to the fungal species diversity of connected organisms. By extrapolation, increasing diversity leads to an increasing infochemical transport. However, this phenomenon would also multiply the number of small and local overlapping networks constituting the overall CMN. This would conduce to an overall decreasing connectivity. The more, the network is long and the more, time to reach the extremities will be important. That why, transfer of organic compounds (carbon and nitrogen) is taking between 1 and 2 days to be forwarded from plant organs to networked fungus and then 3 days to arrive to the receiver (Wu et al. 2002). Experiments have also tested the speed of defence signalling elements in CMN by stopping in the same time the VOCs emission in the air (airborne communication). In this precise case, defence compounds turn out to be faster than nutrients, carbon and water transfers (Gorzelak and al., 2015). In such unlimited pathways, infochemicals could be relayed several times by different organisms after the emission of the first individual (Falik et al., 2012).

It is important to highlight that all the presented findings above have been discovered under lab conditions. Therefore, it may be some differences with what could be obtained when submitted to the diversity of natural settings (Falik et al., 2012).

II. WHY WOULD MYCORRHIZAL FUNGUS ALLOW INTERPLANT COMMUNICATION?

There is currently no doubt concerning the fundamental role of mycorrhizal networks as agents of self-organization (Simard et al., 2015). They established a highly optimized structure which considerably improves and simplifies the natural conditions of interplant communication. However, a question remains recurring: Why fungus would distribute and pass infochemicals (and especially carbon, its vital resource) from one plant to another?

As already presented, fungi are depending on the survival of their host in this mutualistic relation. But, what we are questioning here is the fact that fungal organisms could also survive and be satisfied and of a simple relation with one plant individual. In other words, what is the construction of CMNs really bringing to fungi compared to simple mycorrhiza? What are the reasons to continue the establishment of such pathways and such transfers?

1. A potential co-evolutionary process

Mycorrhiza are known to exist since around 400 million years. These symbiotic relations had probably been possible thanks to the presence of glomales zygomycetous fungi. Presumably, these mutualistic relations were the main drivers of colonization of most ecosystems (Bonfante and Genre (2008). Nowadays, current AMF organisms (and by extension CMNs), would have been the result of these plant–fungi co-evolution through times (Bonfante and Genre (2008). In the other hand, studies like Allen (1996) and Blouin (2018)'s reports, are also pointed out the lack of accurate datas about phylogenetic links and the need of reciprocal approaches to confirm this assumption.

But, in this paper, assumptions are made, claiming that CMNs did persist through such a long time period because of its efficiency to provide fitness advantage to interplant community. And thus, the co-evolutionary process between fungus and plants would represent one potential reason of why would mycorrhizal fungi allow belowground communication and infochemical transfers.

2. Benefits for its own survival

Guarantee free passage of molecular messages is surely one of the best ways to keep plants alive (see on part III) and therefore, insuring fungal survival. The first main difference between CMNs and one-one relation through mycorrhiza is that fungus can take advantage of the interspecific diversity and the number of members constituting the network.

Du to numerous connected plants in the network, fungus is receiving photosynthates (carbon) from several sources. It means that fungus is paying attention about the loss of hosts and try to counter it by making symbiosis with multiple organisms. This low-risk strategy could firstly explain why fungi are preferring doing CMNs than simple mycorrhiza with one individual.

In a second place, facilitating passages of infochemicals (especially defence-related signals) from one plant to another contributes to avoid aphid infestations or predator attacks. The latter considerably affect carbon allocation (Girousse et al. 2005) and by extension, the supply of fungal vital elements. In this case, it is assumed that fungus would do everything, including passing organic compounds from one plant to another, to suppress these threats. In a fungal perspective, infochemical transfers become highly beneficial for its welfare.

In addition, it sometimes arrives that fungus receives more carbon from hosts than it needs to fill its luxury good requirements. In this case, thanks to its capacity of managing resources, fungus is able to send the surplus toward carbon deficital plants in the network. Not only fungus represents a direct contributor of plant survival but also, it retains these plants by encouraging reciprocation. Hence, fungus is clearly multiplying its "carbon portfolios" (Gorzelak et al., 2015). Moreover, it is likely one of the reasons which allows fungal species to deal with uncertain environmental conditions and which is favourishing their establishment in variable ecosystems (Wilkinson 1998).

Assumptions are also made concerning the fact it is greatly advantaging for fungi to access to infochemical flows. Not only for the reasons discussed in the bidirectional control's part, but this phenomenon would also explain why fungal organisms would accept to transfer infochemicals to other plants. Indeed, as a resources manager, fungus could be able to preferentially send defence signalling and nutrient compounds to the best carbon supplier hosts and thus, insuring interplant carbon exchanges (Van't Padje et al., 2016). This has been confirmed with the following experiment (Song et al. 2015): The defoliation of Douglas fir trees causes the propagation of defence signals and carbon toward neighbouring ponderosa pine. This phenomenon had probably been driven by the networked fungus to prevent itself against the loss of healthy and more reliable hosts (its net carbon source).

From another perspective, this experiment also demonstrated that fungus is caring about the interspecific diversity of networked members (Gorzelak et al., 2015). Nowadays, it is admitted that multiple species community are more stable than a single specie group (Perry et al. 2008). Fungus seems to have naturally integrated this principle by promoting diversity within the network and constantly using it, notably in case of danger. In CMNs, diversity is playing a huge role. For example, plants are using resources in a complementary and in a sort of equal way and, thus, are maintaining a very affordable cost for other organisms which want to join the network (Walder et al., 2012). This interspecific diversity is leading toward tit for tat relationships (altruism) among plants and fungi. Philip (2006) noticed existence of such relationships between Douglas fir and paper birch trees and their changing transfer direction of carbon.

III. WHAT ARE THE EFFECTS OF BELOWGROUND HYPHAL COMMUNICATION?

The different roles of interplant communication through mycorrhizal network have partially been presented yet. In this part, it is about to quantify the main effects of underground communication found in the literature. The process of communicating involves at least two organisms, one emitter and one receiver. Here, it is suggested that communication had consequences on both sides.

1. Effects on emitters

Current literature is mainly focusing on receiver consequences of soil communication. It hasn't been mentioned, at any moment, the effects that transferring infochemicals could have on emitters. Thus, it could be interesting to understand, firstly why would plants agree to transfer infochemicals to other? And what are the direct and indirect effects of sending cues and signals for the emitter? Moreover, further researches are needed to determine if communication do have physiological costs on senders.

2. Effects on receivers

Communication processes involve both positive and negative effects on receiver. Some of them have been listed below.

Positive ones

All the following effects can be considered as competitive and fitness advantages for connected organisms by mycelial structures. In fact, CMNs are considerably improving the survival status of networked organisms.

Promoting cooperation and coexistence

Symbiotic relations, and thereby CMNs, are based on cooperation. Every infochemical exchange (except negatives ones) that are occurring through mycorrhizal network, are revealing a high degree of interspecific cohesiveness : a mycorrhizal fungus passing oversupplied carbon toward deficient carbon plants; a belowground defence warning system to prevent damages to other healthy plants; an overall well-oiled machine to provide both luxury goods and scarce resources to every organism in need. There are numerous examples illustrating such cooperation among soil fauna-flora via hyphal pathways. And logically, honest and positive relations naturally involve further cooperation. Several scientists in the field have included these notions within their conclusions. For instance, Read (1997) was affirming that competition doesn't represent the essence of interplant communication and he was encouraging the next experiments to focus on "the distribution of resources within a community". He was, in his report, making assumptions that CMNs are playing a tremendous role in increasing biodiversity and thus, co-existence and cooperation.

To summarize, communication via hyphal connections allows cooperation and coexistence.

Dealing with variable and uncertain environments

Communication also permits networked organisms to cope with variable and unstable ecosystems (Wilkinson, 1998). Each member of the network is connected to at least, one fungal symbiont. The latter is highly adaptable to its direct environment. In case of abiotic and biotic environmental shifts, MFs are able to "guide" their hosts toward best solutions for their own fitness through this communicating fungal network (Gorzelak et al., 2015). Perry et al. (1992) took the example of forest systems into which disruptions of different magnitudes are frequently occurring. These perturbations have significant consequences on interspecific community structure. Here, the mycorrhizal fungus and members of the CMN are both helping each other via belowground communication means. The fungal organism uses it to, strategically, increase the number of its hosts and thus, ensure a permanent carbon supply even if environmental conditions are rude. In the other hand, plants are maintaining the fungus alive by taking care of each other and by relying on the interspecific biodiversity of the network. These phenomena are resulting to "groups or guilds, of plant that are interlinked though a common interest in a mycorrhizal fungi".

Increasing defence signalling and disease resistance

As presented in the first part, CMNs allow defence signalling molecule transfers in case of herbivore attacks. Indeed, lots of experiments in literature demonstrated physiological and defensive changes within a healthy herbivore-free plant neighbouring an injured host, both related to a CMN (Van't Padje et al., 2016; Babikova et al., 2013). For example, aphid infested plants will warn all the surrounding organisms by sending infochemicals through fungal pathways (Babikova et al., 2013). These molecules will provoke the secretion of repellent or toxic compounds within aphid-free plants, aimed to deter enemies from attacking or limiting damages. In the same time, non-networked organisms would also be directly concerned by this defensive process (notably via the diffusion of VOCs) such as aphids itself and aphid parasitoids. Indeed, antennae of both insects would have an increased electrophysiological activity and parasitoids would be attracted to pea aphids (Babikova et al., 2013). Thereby, relaying defensive informations through CMNs seriously affects plants, herbivores and natural herbivore enemies' behaviour. This phenomenon greatly influences multitrophic interactions (Babikova et al., 2013).

Belowground mycelial network can be seen as complementary with the airborne defence system and plants are using both ways together simultaneously. Thus, hyphal interplant connections seem to play a role as much important as the aerial warning process in defensive situations. Interestingly, effects of belowground warning transfers last even when aerial signalling compound emissions are quite limited or have been stopped since a long time ago (Barto et al., 2012). Plants appear to be able to switch between these two communication means when environmental conditions are unfavourable to use them in the same time. Indeed, aerial or underground transfers can be easily blocked by experimental designs (Gorzelak et al., 2015), simulating a disconnection of the MN or the plant isolation in a particular environment. In this case, plants prevent any rupture by communicating via the other valid way. However, further researches need to deepen which defensive way remain the more widely adopted within plant community and which one is the most competitive.

An optimized defensive signalling system isn't only about protecting from herbivores but also from pathogens and fungal diseases. Assumptions are made that CMNs could vehicle signals which lead to an increased plant defence against diseases. Accordingly to Song et al‘s experiment (2010), healthy tomato plants linked via CMN with infested leaf early blight plants would get an improved physiological functioning like a boosted enzyme activity, a higher pathogen resistance and the activation of particular genes dealing with defense issues.

Mycorrhiza are permitting an improvement of surrounding plant lifetime, by conveying defence signals. Usually, plants living closer may compete for local resources (sun, water, nutrient...). In this case, it appears evident that interplant proximity remains more beneficial than living by itself. In fact, the diffusion of warning compounds via MNs may lead to the profusion of healthy and resistant plant groups which may be less vulnerable to attacks and diseases. Each vegetal organism is creating its own shield to protect itself (Barto et al, 2012).

Here, communication allowed by MF represents a complex and highly performing system which implies physiological shifts at different trophic levels without direct links with predators or pathogens.

Favouring genetically related plants

There is a growing body of evidences that genetically related plants are helping each other to grow and insure viable life conditions. And MNs turn out to be very interesting from this perspective. Indeed, recent studies highlighted the big role of hyphal connections for kins. These studies mainly concern AMF networks (the most ubiquitous ones). First, plants connected with kins via a CMN are showing improved characteristics. Experiments dealing with *Ambrosia artisifolia L.* linked with related plants was presenting a higher rate of foliar nutrition than in normal conditions (networked with strangers) (Gorzelak et al, 2015). Thus, kins seem to create and implement their own fitness advantage by passing more carbon from older plants to younger seedlings than to non-genetically close plants which are members of the network. Gorzelak et al (2015) are assuming that kin selection is frequently occurring with limited seed dispersal plants. In this case, there is a high probability to establish a parental relation between old plants and surrounding seedlings. Thanks to the CMN, carbon is easily exchanged between these two entities (from the older to the younger). Here, older donors are self-sacrificing to provide carbon which will benefit to the youth's genetic fitness. It is about ensuring that common genes would be transmitted from generation to generation. This theory is widely confirmed by experiments on Douglas fir trees. Gorzelak et al (2015) quantify the amount of transferred carbon and nutrients from one individual to related organisms and also the mycorrhizal colonization rate. And it has been demonstrated that all these parameters were bettered when it was a kin receiver, especially concerning carbon transfers which were two times higher than in normal conditions (Gorzelak et al, 2015). Hence, Douglas fir trees are compared to clonal plants caring about the fitness of the gene pool and its evolution. Like *Betula nana* plants (clones) are doing in arctic tundra, shuttling about 5% of all the photosynthetic carbon for supplying relatives through CMN (Deslippe and Simard, 2011).

Second, several studies are affirming that kin signaling are based on honesty and thus, are better taken into consideration by receivers. Logically, it is admitted that individuals are more willing to send honest informations to relatives which share common goals and interests (saving genes) than strangers (Van't padje et al., 2016). For example, concerning defense-related signals, the closer plants are, more similar the emitted belowground VOCs profile is. And plants are inclined to answer to messages which are similar to their own (comparable molecular profiles of both emitter and receiver's messages). Hence, information coming from genetically related organisms, is considered as reliable (Karban et al., 2013).

Negatives ones

CMNs have been shown as the perfect mean for cooperation and co-habitation with very frequent infochemicals exchanges contributing to each member survival. However, MNs are not only the place of win-win relations but also negative ones for receivers (win-lose interactions).

Allelopathic interactions

As presented in the first part, mycelial connections are possibly conveying allelopathic compounds. In which extent, are belowground allelopathic element transfers impacting plant population within the network? Several studies have recorded effects through both AMF and EMF networks (Barto et al., 2011; Cipollini et al., 2012) since the first findings 45 years ago. Barto et al. (2011; 2012) pointed out a significant loss of surrounding plant biomass caused by the diffusion of marigold allelochemicals via hyphal pathways. In this case, inhibitors (like juglone) seem to counterbalance all the positive effects brought by CMNs (especially the nutrient supply) and become predominant. Here, allelochemicals provoke direct effects on plants but some other experiments are showing indirect consequences.

Indeed, soil microbes can also be targeted by allelopathic compounds which would indirectly influence neighbouring plant environmental conditions. The sender is then considerably advantaged because by attacking microbial fauna, it would block all the nutrient, carbon, water and mycorrhizal infochemical fluxes at the expense of competing organisms. Not only the emitter is suppressing its rivals but also it does not expose and harm itself. This is highly beneficial (competitive advantage) if the sender does not require symbiotic fungi or bacterias to survive. To illustrate, the example of *Alliaria petiolate*, an EMF and AMF invader that does not need symbiotic associations, can be quoted (Achatz and Rillig. 2014). This plant is mainly proceeding by limiting colonization (through a spore germination inhibition and a decreasing functioning of physiological plant characteristics) of fragile soil mycorrhizal communities within unfavorable ecosystems. Logically, CMN-dependent plant populations are progressively declining, thereby allowing a rapid colonization by Alliaria. Many experiments revealed that alliaria allelochemical efficiency is depending on the emitter age and its density. For instance, the more the sender is young, the more, allelopathic potential is high (Achatz and Rillig. 2014). Many other factors like the degree of mycorrhizal dependence of targeted plants and the evolution through history of the abiotic and biotic soil properties may play a fundamental role concerning the allelochemical efficiency on other soil organisms (Cipollini et al., 2012).

Still dealing with indirect effects of allelochemicals, soil microbes can unintentionally mediate their effects in a positive or negative way when they are not damaged by these molecules. For instance, microbial degradation of allelochemicals is followed by a decreasing harmful potential. But in the opposite way, it can sometimes arrive that the resulting degradation product is more deleterious than the initial molecule (Cipollini et al., 2012).

It is also the case for plants which can elaborate physiological strategies to limit negative effects. Cipollini et al. (2012) are mentioned enhanced plant resistance over time to such chemicals.

Hence, allelopathic interactions are not as simple as previously presented above. Their efficiency is greatly dependent on environmental settings (concerning both receiver and sender and the ecosystem into which they are evolving). Each allelopathic plant specie seems to present particular parameters and thereby involves further researches to discover them all.

In a nutshell, allelochemicals are leading to great consequences concerning seed germination, reproduction, plant physiological development and spatial distribution of both vegetal and microbial species. That's why, Achatz and Rillig (2014) qualified allelopathic molecules as structuring agents of microbial and interplant communities.

Releasing allelochemicals isn't the only way for inhibit networked member growth. Indeed, accordingly to Barto et al. (2011), seedling connections to a MN could have inhibitor consequences on their growth. In fact, there could be an unbalanced amount of transmitted carbon from young seedlings toward the networked fungus. Hence, plants would not possess enough carbon for fulfilling their own vital requirements. Seedlings appear to be disproportionally drained and CMN, in this case, does not represent a fitness advantage for its members.

Cheating, eavesdropping and exploitation of the information

Within plant communities, information fluxes, are not always arriving to the initial targeted plant, especially dealing with this complex interactional environment represented by the rhizosphere. Indeed, when plant individuals are emitting infochemicals through CMNs, these molecules are considered as "public goods" (Van't Padje et al, 2016): Every member of the network is, thereby, able to use it for its own benefit even if these organisms were not the initial recipient. Studies pointed out that parasitic plants, like myco-heterotrophs, are doing such things to survive. Hyphal pathways, perfect environments for cheating, allow them to gain resources in an easier way without paying the true cost of joining. These plant cheaters can eavesdrop on sent information, extract as well as luxury goods as scarce mineral elements. They also developed mimic cooperative signal systems (Van't Padje et al, 2016) for passing themselves off as honest, authentic and truly contributors of the mycelial network. The first victims of such actions are the initial targeted plants which would be amputated from their vital resources while they are entirely paying the cost of being included within CMN (Simard et al., 2015).

To conclude this final part, Bais et al (2004) indicated that consequences of most infochemical transfers into soil haven't been observed under natural conditions. Hence, further effects of belowground communication could be clarified or discovered in future experiments which would be realised in closer natural settings.

LIMITS AND DISCUSSION

During this bibliographic work, the most recent review that has been found, is dated from 2004 (Simard and Durall, 2004). In this paper, the authors are focusing exclusively on carbon exchanges and are compiling some knowledge related to the functioning and the role of CMNs. It doesn't refer to the term of communication processes and it's clearly specialized on carbon fluxes. In contrast, what has been done here, is to describe in more broadly terms what represents belowground communication. Thus, Simard and Durall's review can constitute a complementary element to understand in a better way the nature of nutrient transfers. It doesn't deal with the same study questions, that's why our review remain interesting.

But, this synthesis is also bringing to light several biases in interplant communication study fields.

The first limit remains the vague definition of communication. Indeed, in the introduction part, it is presented that scientific community is still debating on how communication mechanisms should be described when concerning plants. In order to give a broad overview of new findings in the field, the most general definition of communication namely "*Communication is driven by the exchange of substances released by one organism and detected by another*", from Barto et al's report (2012), constitutes the basis of this review. Hence, this choice could be easily criticized, arguing that too many physiological mechanisms could be included within this definition whereas they aren't related to any

communication processes and plant intention to communicate. For instance, nutrient transfers such as carbon, phosphorus and water represent one of these physiological mechanisms which could be questioned.
Due to this unprecise definition, the limit between animal and interplant communication appears to be completely confuse. Hence, most of articles are proposing an anthropomorphism point of view of plants-fungi interactions. Both organisms are presented as thinking individuals which entirely integrate notions like trading, manipulating and handling resources. However, none of the articles are demonstrated scientific proof to confirm that plant level of consciousness. This anthropomorphism may discredit all the solid experimentations presented above. It also implies many future findings to elucidate and precise interplant communication.

Even if this review comprises few limits, some gaps have been identified all along this report, suggesting extensive researches on the following topics:

Thematic	Avenues for researches
The nature of transferred compounds within CMNs	Identify and provide an accurate listing of all the possible transported molecules.
Infochemical transportation through fungal structures	Determine which pathways are the most likely to be used by infochemicals. Get more datas on polarity and size restriction of transported molecules.
Degree of control of infochemical transfers by plants and fungi	Determine if transfers are resulting from an intentional or involuntary process.
The scope of infochemicals	Characterize the propagation time of all the categories of conveyed molecules from plant organs to MF and then from MF to targeted plant (only carbon and phosphorus propagation time have been precisely presented yet).
Experimentation conditions	Reproduce and test scientific assumptions under natural settings.
Symbiosis evolution	Clarify the co-evolutionary process between MF and plants.
Effects of interplant communication	Elucidate effects of sending infochemicals from the emitter perspective.
	Qualify the effects of such belowground communication on biotic and abiotic properties of soils.
Application	Integrate these findings within human technology such as biomimicry.

Figure 3 : Summary of gaps which need to be investigated

Finally, this review is taking into consideration over 40 references, a reasonable amount of studies which is sufficient to present credible informations. But, it is also important to notice that, with the scientists' recent interest about interplant communication, numerous articles have been posted lately and probably containing new discoveries that haven't been discussed in this review.

CONCLUSION

This bibliographic synthesis was enough to understand the tremendous role of MF in enhancing underground communication among plant and the entire soil fauna. Plentiful studies do exist dealing with this topic and thereby, this compiling work is only scratching the surface of what has been discovered and experimented. However, it also permits to have a quick look on what should be pursued. The deepened aim of this paper was to open mind about what is invisible namely communication processes and underground networks. The importance of taken into account plant interactions and belowground communication networks is already giving ideas for human applications notably in the agricultural field. Indeed, considering hyphal networks would maybe question conventional farmers and agronomists about ploughing practices. Related to this issue, further work should be done about the mycelial robustness by soil biota (Barto et al., 2012) and human ploughing methods. Moreover, many studies (Babikova et al., 2013) are also revealing that the highly optimized signalling defence system and disease resistance du to both above- and below-ground communication, could have a significant effect on the removal of insect pests in fields. In fact, most crops species are together linked with AMF (Simard et al., 2015) so it could be a fabulous searching area for improving agricultural production and handling insect pests (Babikova et al., 2013). In addition, as suggest Walder et al., (2012), farmers who don't have enough resources to continue implementing traditional agricultural technics, are unintentionally already counting on hyphal connections to boost yields. Therefore, a maximal optimization of CMNs (and systemic approach of soils) could be a sustainable and affordable way to increase agro-system overall productivity for resource less farmers and thus supply the worldwide growing food demand (Walder et al., 2012).

Future applications are not all focusing on agriculture but also in urban planning and road design. In fact, it is possible to get inspired of fungal networks which are presenting unprecedented adaptable and reforming characteristics in function of direct environmental shifts. Such biomimicry could potentially be applied to congested bypasses (Bais et al., 2004) in Europe for example.

Still on a looking-forward vision, current studies have demonstrated the great consequences of biotic an abiotic environmental parameters such as resource availability on plant sensitivity to molecular transfers (Pezzola et al., 2017). In this context of climate change, preventing measures should be taken for avoiding detrimental implications on interplant communication. For instance, Barto et al., (2012), tried to predict effects of the increasing amount of atmospheric CO2 on underground communication. It appear to enhance AMF length connections into the rhizosphere. By expansion, it means that climate change would probably increase the overall supply of infochemicals within networks. In the other hand, more and more nitrogen compounds are polluting soils which provoke an over-mortality of mycorrhizal fungus according to Bais et al. (2004). Fungal specie population are declining before having been discovered and as well as all the ecosystemic services they provide. But paradoxically, botanists seem to be blind to their future potential extinction and refuse to designate them as conservation objects (Bais et al. (2004)).

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Interplant communication

The role of mycorrhizal networks concerning underground interactions

Résumé :

Depuis les 40 dernières années, la communauté scientifique est en ébullition. Les récentes observations d'une possible communication chez les plantes a permis l'émergence de découvertes fondamentales dans le domaine de l'écologie. Ainsi, deux conclusions ont pu être mises en évidence. Les plantes peuvent interagir de manière intra spécifique et inter spécifique. De plus, elles ont aussi bien la capacité de communiquer de manière aérienne que souterraine. La plupart des chercheurs s'accordent à définir la communication dans le monde végétal comme étant : l'échange de composés chimiques (information) entre un individu émetteur et un individu récepteur (Barto et al., 2012). La découverte des mycorhizes (association symbiotique entre plante et champignon au niveau des racines) en 1885 et celle des réseaux mycorhiziens reliant plusieurs plantes entre elles, près d'un siècle plus tard, représentent un pas significatif dans l'étude des interactions faune-flore souterraines. De nos jours, il semble admis par tous que la communication souterraine par le biais de ces réseaux mycorhiziens, représente un des principaux facteurs améliorant l'avantage compétitif des plantes faisant partie de ce réseau et de leurs potentialités de survie. Cette revue bibliographique a pour but de donner un aperçu des récentes découvertes dans ce domaine ainsi que des pistes de réflexion futures.

Mots Clés : Communauté végétale et fongique ; communication souterraine ; réseaux communs de mycorhizes ; composés chimiques d'information