Arbuscular mycorrhizal dialogues: do you speak 'plantish' or 'fungish'?

Arbuscular mycorrhizal dialogues: do you speak *plantish* or *fungish*?

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Key words

Arbscular mycorrhizal fungi; chitin; strigolactones, cutin monomers, signal molecules, receptors

Highlights

Plant microbiota - Similar to human microbiota, in plants, microbial communities thrive in tissues and on organ surfaces (e.g. in the rhizosphere and phyllosphere), cooperating in key metabolic processes and creating a network of mutual relationships. To date, most research on plant microbiota has focused on bacteria, identifying dominant communities of Actinobacteria, Bacteroidetes, Firmicutes, and Proteobacteria. However, eukaryotes such as fungi, with lifestyles ranging from mutualism to parasitism and commensalism, also make up key components of the plant microbiota.

Arbuscular mycorrhizae - Among plant-associated microbes, the widespread arbuscular mycorrhizal fungi play a key role in nutrient cycling and plant health due to their ability to improve plant mineral nutrition. These fungi belong to an ancient monophyletic phylum, the Glomeromycota, currently considered to be phylogenetically related to the Mucoromycotina. Unusually among fungi, Glomeromycota are obligate biotrophs, multinucleate, and apparently asexual. Analysis of the genome sequence of *Rhizophagus irregularis* revealed additional unique features, e.g. the absence of plant cell wall-degrading enzymes and the abundance of small, secreted proteins.

Plant immunity - Plant immunity relies on cell-autonomous events with some similarity to the innate immune system in animals. Plants use extracellular receptors to recognize microbe-associated molecular patterns (MAMPs, e.g. bacterial flagellin) as well as endogenous molecules (such as wall oligomers released during pathogen attack), activating MAMP-triggered immunity. A second level of perception drives effector-triggered immunity, which uses intracellular

receptors to recognize pathogen-secreted molecules called effectors. The high variability and specificity of effectors feeds plant-pathogen co-evolution.

Conservation of symbiotic signaling - In arbuscular mycorrhizal host plants, a conserved signal transduction pathway mediates the perception of fungal signals. The proteins characterized so far include a membrane receptor-like kinase, a mevalonate biosynthetic enzyme, nucleoporins, a cationic channel localized to the nuclear envelope, and a nuclear calcium/calmodulin-dependent kinase. In legumes, the same proteins also participate in the signal transduction pathway mediating the perception of the rhizobial Nod factor during nodulation, *via* a common symbiotic signaling pathway.

Abstract

Plants rely on their associated microbiota for crucial physiological activities; realization of this interaction drives research to understand inter-domain communication. This opinion report focuses on the arbuscular mycorrhizal (AM) symbiosis, which involves the Glomeromycota, fungi that can form a symbiosis with most plants. We examine the hypothesis that the molecules involved in inter-kingdom symbiotic signaling, such as strigolactones, cutin monomers, and chitin-related molecules, also have key roles in development, originally unrelated to symbiosis. Thus, their symbiotic roles rely on the co-evolved capacity of the AM partners to perceive and interpret these molecules as symbiotic signals.

In cartoons, animals, plants, and mushrooms communicate with each other flawlessly. However, in real life, understanding how individuals belonging to different domains of life communicate, via ‘plantish’ or ‘fungish’, remains a hot topic in the field of plant-microbe interactions. Plants and microbes exchange signals that regulate each other’s metabolism and development, and ultimately condition their interactions. Several examples of inter-specific communications have been identified in the hidden world of plant-microbe interactions. One long-known example is the perception of Nod factor from rhizobial bacteria, by legumes; this perception ultimately leads

to the generation of a novel symbiotic organ, the root nodule, where symbiotic bacteria fix atmospheric nitrogen into organic compounds (1). More recently, exciting new projects aim to introduce symbiotic nitrogen fixation in cereals (2; https://www.jic.ac.uk/news/2012/07/cereals-self-fertilise/#), which requires a deep understanding of this inter-domain signal exchange.
Plant-microbe communications rarely occur as one-to-one conversations, since plants host large and diverse microbiota, which offer beneficial ecological services to their green host. The association with microbiota also requires that plants modulate their immune system, in order to tolerate, stimulate, or counteract the activities of myriad soil microbes, each producing their own signal molecules (3).

A common question in the plant biology literature is: '*How do plants identify microbes as friends or foes?'* (4). On this topic, the arbuscular mycorrhizal (AM) symbiosis is an excellent model to discuss the exchange of signaling molecules at the inter-kingdom level (5): AM fungi are the most widespread fungal component of the plant microbiota, and most land plants support an AM symbiosis, irrespective of their phylogenetic position (6), suggesting the existence of a conserved communication process.
Here, we summarize the characteristics of the best-known plant and fungal molecules that trigger symbiotic responses in the corresponding AM partner. Interestingly, the signaling molecules characterized so far (strigolactones, cutin monomers, chitin-related molecules) appear to have well-established developmental roles, unrelated to symbiosis, in the organisms that produce them (Fig. 1).

Host plant signals to AM fungi: *¿Hablas plantish?*

Strigolactones, terpenoid lactones that derive from carotenoid metabolism (Fig. 2), were first studied as root-exuded molecules that elicit the germination of parasitic plants (7); more recently, strigolactones returned to the limelight as bioactive molecules that stimulate the branching and metabolism of presymbiotic hyphae in AM fungi (8; 9). Finally, strigolactones emerged as key plant hormones that repress shoot branching by controlling axillary bud growth (10) through a well-characterized, receptor-mediated pathway that probably interacts with other plant hormones (11). Strigolactone production is conserved from Charales to Embryophytes,

including the basal groups of liverworts and mosses (12). These discoveries have revolutionized our view of strigolactone signaling: their function in the rhizosphere suddenly appearing to be a secondary feature relying on their leakage from the roots into the soil (13). Thus, ten years after the seminal studies by the Akyama (8) and Bécard (9) groups, emerging data suggest that strigolactones function as conserved determinants of plant development that were recruited during the evolution of plant symbiotic and parasitic interactions.

Despite this emerging interest, our knowledge of strigolactone perception by AM fungi remains very limited. Besserer et al (9;14) demonstrated that strigolactone perception boosts fungal metabolism, leading to increased ATP production and mitochondrial division. Preliminary data from RNA-seq of germinated spores of the AM fungus *Gigaspora margarita* treated with the synthetic strigolactone GR24 confirm the upregulation of mitochondrial genes (A. Salvioli, P. Bonfante et al unpublished results). Interestingly, strigolactone treatment also induced the proliferation of *G. margarita* endobacteria (15). Furthermore, by introducing the calcium sensor TAT-aequorin in the same fungus, Moscatiello et al (16) demonstrated that GR24 causes a rapid calcium transient in the fungal cytoplasm. Finally, GR24 treatment of *G. margarita* and *Rhizophagus irregularis* (17) increases the release of short chito-oligosaccharides, pre-symbiotic fungal signals, as discussed below.

In short, recent data suggest that AM fungi perceive strigolactones through a calcium-mediated pathway and activate multiple responses involving fungal cell wall-related metabolism (hyphal branching and chito-oligosaccharide production), and mitochondrial and endobacterial activity. However, fungal strigolactone receptors remain unknown and analysis of the *R. irregularis* genome (18; 19) and *G. margarita* transcriptome (A. Salvioli, P. Bonfante et al., unpublished results) have not revealed the existence of fungal homologs of the known strigolactone receptors in plants (11). Thus, we can only conclude that fungal and plant strigolactone receptor proteins likely differ in structure, which opens the possibility that AM fungi independently evolved strigolactone perception mechanisms.

Recent work identified cutin monomers as plant signals that have a key role in the AM dialogue (Fig. 2). These hydroxylated aliphatic acids are proposed to be released on the root surface as a necessary signal for hyphopodium differentiation from presymbiotic AM fungal hyphae (20; 21). Direct evidence showed that hyphopodium development requires the function of RAM2, a *M. truncatula* glycerol-3-phosphate acyl transferase involved in hydroxylated aliphatic acid biosynthesis, and is enhanced by the application of exogenous cutin monomers.

Cutin polymer is the major component of the cuticle, the waxy coating of aerial organs in land plants: cutin also has a well-known role as a signal to pathogenic fungi that attack leaves, stems and fruits (22). A novel role for this hydrophobic molecule in a hydrated, underground environment such as the root surface may sound surprising. On the one hand, this suggests the existence of unpredicted similarities between symbiotic and pathogenic interactions, independent of the target organ (23); on the other hand, the fact that all plant clades that produce cutin (from liverworts to angiosperms) also develop AM interactions (6) is a suggestive coincidence. So far, however, no evidence points to a direct relationship between hyphopodium development and the presence of cutin monomers on the root epidermis wall (24), nor to the perception of cutin by AM hyphae: in other words, we cannot exclude the possibility that cutin monomers act upstream of a cascade of plant responses controlling hyphopodium development through other, unidentified signals.

Fungal signals to AM host plants: *Parlez-vous fungish?*

Navazio and colleagues (25) provided the first evidence of diffusible signals in the exudates of germinated glomeromycotan spores (GSE), showing that treating soybean cultured cells with concentrated GSE induced - within minutes - a transient increase in cytosolic calcium concentration with a characteristic profile. They also showed that GSE did not trigger the production of reactive oxygen species, a typical response to exudates from pathogenic fungi. Also, nitric oxide accumulates in the first minutes after GSE application to *M. truncatula* roots (26) and GSE triggers nuclear Ca^{2+} spiking with the same timing (27). The first analyses of plant gene regulation showed that *Enod11,* a *M. truncatula* nodulin expressed in legume roots during early nodulation, was also upregulated in response to diffusible fungal signals (28). In this case, the experimental setup did not allow a precise timing of this response, but in a later work, Maillet and coworkers (29) showed that 30 h treatment with GSE triggered *Enod11* expression. On a longer time frame, the perception of diffusible fungal signals induces reallocation of sugars within the plant, with the accumulation of starch in the root system (30). The most recent studies identified secreted molecules that are supposed to play a role in fungal signaling to the host plant. These include (Fig. 2), lipo-chito-oligosaccharides (LCOs; 29) andchito-oligosaccharides (COs; 17). These molecules trigger GSE-like responses in the host roots, including Ca^{2+} spiking (17), and the regulation of symbiosis-related genes (29; 31).

An interesting aspect of fungal signaling is that LCOs and COs both have structures closely related to chitin. This raises the question of whether the production of such molecules occurs as a direct by-product of fungal cell wall biosynthesis or evolved from it *via* the generation of specific metabolic pathways. In either case, molecules related to fungal cell wall biogenesis play a role as inter-kingdom messengers that only AM host plants recognize as symbiotic signals (17).

The idea that AM fungal signaling is based on chitin oligomers raises a critical specificity issue: since all fungi produce N-acetyl-glucosamine chains of various lengths, how can plants identify each fungus and raise the appropriate response, discriminating between a symbiont and a pathogen? As a further complication, the major rhizobial signals, the Nod factors, have a striking structural similarity to LCOs, including the same N-acetyl- glucosamine backbone (32). Indeed, plants have large families of receptors and receptor-like proteins that are predicted to bind chitin-based molecules, including the bacterial Nod factors (33). They all possess conserved lectin-like, chitin-binding LysM domains, but the specificity of each receptor for each chitin oligomer in native conditions remains to be fully understood. Overall, the picture will likely remain obscure until we understand how these receptor proteins act, either alone or within complexes, in different plants and in the presence of different combinations of ligands (34). At any rate, such a massive deployment of plant genomic resources, deriving from extensive gene duplication and neo-functionalization (35) can indicate a diversified perception system, acting upstream of MAMP-triggered immunity and symbiotic responses, and representing a possible key to plant recognition of each interacting microbe.

Dr. Dolittle in the rhizosphere? Plants and AM fungi speak to each other

Although our knowledge of symbiotic signal exchanges in AM remains limited, an intriguing speculation appears reasonable: during their long co-evolution, glomeromycetes and their host plants seem to have developed the ability to intercept structural or hormonal molecules from their respective partner and interpret them as symbiotic messengers. Along this line, the similarity of strigolactone and abiotic stress-induced Ca^{2+} transients recorded in *G. margarita* (16) suggests that fungi first perceived the *plantish* strigolactones as natural xenobiotic compounds. It will be extremely interesting to understand whether other plant-interacting fungi (including pathogens) have analogous responses.

We can construct similar speculations about *fungish* signals: fungi produce chitin for a structural

function, but the host plant interprets chitin as a signal. Moreover, a more complex picture surfaces in this case. First, AM fungi possess several chitin synthases (according to Tisserant et al, 18), possibly related to the different arrangement of chitin chains in the thick, layered wall of spores or the thin, loose walls of arbuscule branches (37; 38). Which of these enzymes are responsible for CO and LCO biosynthesis? Can we compare the long-chain chitin fibrils present in fungal walls with the short (probably diffusible) COs that are recognized as MAMPs by LysM receptors (39)? How can chitin-based molecules elicit both symbiotic (e.g. nuclear calcium spiking) and defense responses (e.g. expression of pathogenesis-related proteins) as expected in the innate immune response (40)? Replies to these questions are expected from the ongoing characterization of the plant receptor and receptor-like protein families, which are predicted to bind chitin-based molecules (41), and from a deeper biochemical characterization of fungal and plant bioactive molecules (42).

At present, a simplistic view suggests that plants interpret short-chain chitin-derived molecules (CO4-CO5; LCOs) as symbiotic signals, while longer molecules (e.g. CO8) elicit defense responses; nevertheless, early responses based on transcriptomic (Giovannetti et al., unpublished), cellular, and physiological analyses (43) indicate a partial overlap between symbiotic and pathogenic signaling. For example, root treatments with 10^{-8} M CO4 trigger symbiotic Ca^{2+} spiking in AM host plants like *M. truncatula* or *D. carota*, whereas 10^{-8} M CO8 does not (17). Nevertheless, at 10^{-5} M, both molecules activate the symbiotic response in tomato and rice (43), suggesting that such high concentrations can compromise specificity of perception, possibly depending on the plant host (e.g. legumes *vs*. non-legumes) and on the degree of crosstalk within the LysM receptor family.

Another crucial point is to understand if the chitin-based *fungish* words we have discussed so far are associated with other powerful signals such as fungal effectors, i.e. small secreted proteins. Pathogenic fungi use effectors to interact with their hosts, in some cases targeting the host nucleus and interfering with plant gene expression. We still do not know whether effectors are as important in mycorrhizal as in pathogenic fungi; although the *Rhizophagus* genome contains many small, secreted proteins (18), most remain to be characterized (44). Altogether, it is intriguing to think of chitin - chemically spelled in shorter or longer versions - as the *fungish* word for "hi", a common, non-committing signal making the first connection, with just a hint of the beneficial or pathogenic attitude of the visitor. Specificity might rather rely on the action of effectors, reaching the nucleus and going deeper inside the plant cell mechanisms to drive the major responses, in a process reminiscent of the well established zig-zag model of plant-pathogen interactions (45).

We are tempted to conclude that fungi speak *fungish*, and plants speak *plantish*, but members of the opposite kingdom interpret their chemical words with a different meaning - a picture far from the dialogues between the cartoon characters of our childhood. Nevertheless, pre-symbiotic signal exchanges in AM symbiosis seem to bring some light: the perception of strigolactone by germinated spores of *R. irregularis* or *G. margarita* causes an increase in the production of short chain COs, which in turn trigger a stronger Ca^{2+} spiking response in the root epidermis (17). This chemical dialogue proves that, at this point in their long co-evolution, plants and glomeromycetes have learnt to understand each other.

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Figure captions

Figure 1. Our current view of the signaling between arbuscular mycorrhizal fungi and their host plants suggests that molecules with a developmental role in each organism have been intercepted by the respective partner and re-interpreted as symbiotic signals.

Figure 2. Plantish and fungish signals. The establishment of the arbuscular mycorrhizal symbiosis culminates in the development of arbuscules (central panel), where the fungal and plant cells intertwine to create a symbiotic structure in its truest sense. Similarly, the chemical dialogue between the two symbionts is based on an exchange of *plantish* and *fungish* words that get a novel meaning in the context of the symbiosis, as compared to the structural (cutin, chitin) or hormonal (strigolactone) roles that the same - or closely related - molecules play in the producing organism.

Figure 1

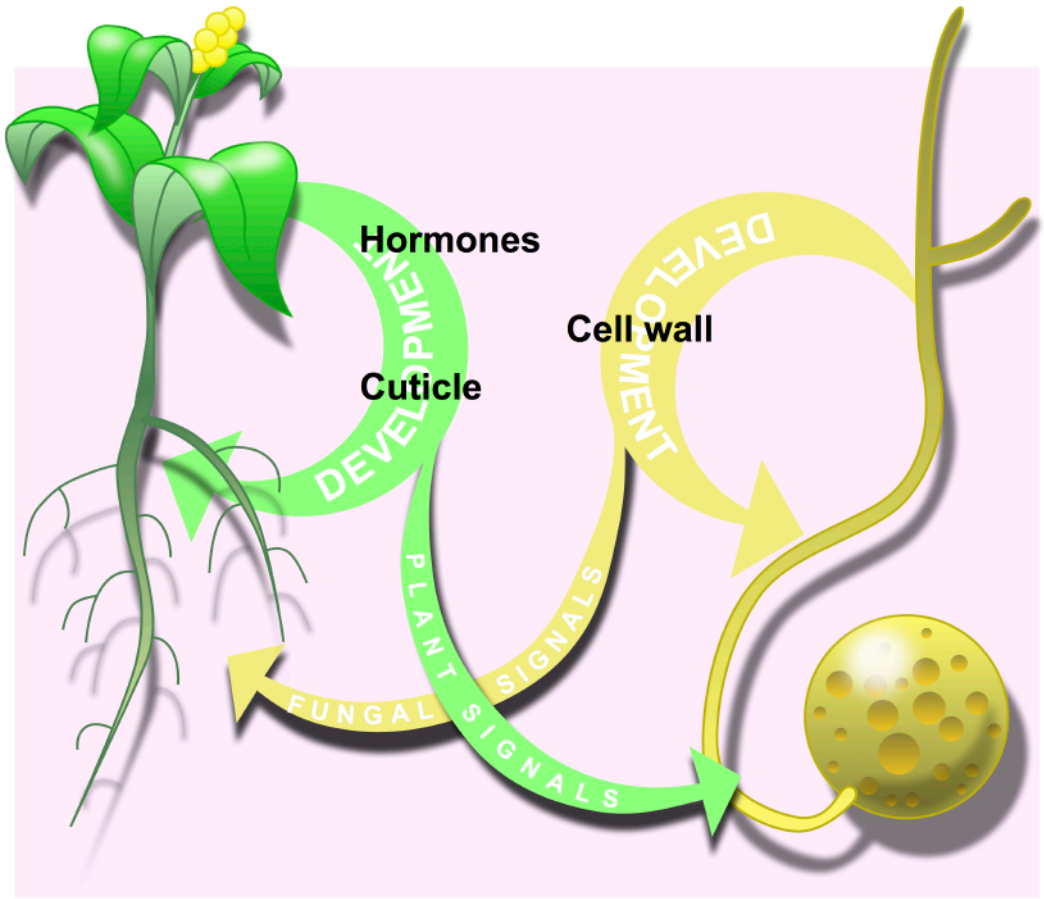

Figure 2