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Signals and cues in the evolution of plant–microbe communication

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Communication has played a key role in organismal evolution. If sender and receiver have a shared interest in propagating reliable information, such as when they are kin relatives, then effective communication can bring large fitness benefits. However, interspecific communication (among different species) is more prone to dishonesty. Over the last decade, plants and their microbial root symbionts have become a model system for studying interspecific molecular crosstalk. However, less is known about the evolutionary stability of plant–microbe communication. What prevents partners from hijacking or manipulating information to their own benefit? Here, we focus on communication between arbuscular mycorrhizal fungi and their host plants. We ask how partners use directed signals to convey specific information, and highlight research on the problem of dishonest signaling.

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Introduction

From quorum sensing bacteria [1] to singing whales [2], organisms across the tree of life rely on communication systems to convey information. Broadly defined as the 'completion of corresponding signals and reactions' [3], communication plays a key role in the evolution of organisms and the complexity of life [4]. On an individual level, communication affects behavioral responses, which affects the fitness of both sender and receiver. From an evolutionary vantage point, this is important because organisms can engage in 'honest' communication or they can manipulate information for their benefit [5].

Theory predicts honest signaling to be favored when (i) individuals share a common interest, such as when they are kin and (ii) when signals carry reliable information that is correlated with something useful to the receiver [6••]. However, when communication occurs outside related kin, for example among different species in symbiotic partnerships, communication systems can be vulnerable to exploitation [5]. Effective crosstalk is necessary to form the partnership, but partners may coerce each other to behave differently by manipulating information to their benefit.

In recent years, there has been an increasing interest in communication among plants and microbial root symbionts [7–9]. Plant roots are surrounded by a multitude of soil organisms, whose diversity covers tens of thousands species [10]. How can pathogen invasion be prevented while beneficial partners are encouraged? While work in the last decade has led to a detailed knowledge of molecular crosstalk in the rhizosphere [11], we do not understand the evolutionary origins and stability of rhizosphere communication. This is a major point of interest because deceptive organisms, such as those that mimic signals to gain host resources [12], or those that interfere with plant signaling to increase their own fitness at the expense of the plant's [13,14], are predicted to spread throughout populations of cooperators [15••]. What prevents the hijacking or manipulation of communication systems?

Our aim is to explore evolutionary aspects of plant–microbe communication, specifically asking: when are communications systems vulnerable to exploitation? We will focus on the symbiosis between arbuscular mycorrhizal (AM) fungi and their plant hosts, where plant carbon is exchanged for soil nutrients from the fungus. This symbiosis is among the most widespread (utilized by ~70% of all vascular plants), and estimated to have evolved roughly 450 MYA [16]. Evidence is accumulating that signaling pathways initiating the AM symbiosis are ubiquitous across extant land plant lineages [17], and are so successful that the components have been recruited by plants to evolve other symbioses, such as rhizobial N_2-fixation [18].

Signal versus cue: why does it matter?

To understand the potential for exploitation in plant–microbe communication systems, it is important to define the differences between signals and cues [19]. A signal is a behavior that has evolved to convey information about the signaler or its environment. In turn, the transferred information changes the behavior of the receiver (Figure 1). This implies that a behavior change is positive, and provides a fitness benefit to both sender and receiver.

Figure 1

Strigolactone as:	Signal	Cue
Evolved owing to effect on the sender?	Yes	No
Benefits the receiver to respond?	Yes	Yes
Example	AM fungal colonization 	Parasitic plant infection 
To demonstrate that a substance is a signal and not a cue, it must be shown that it evolved because of the response it elicits.	Roots actively emit strigolactones as a signal to attract AM fungi. The fungi respond to the signals by growing towards the root, initiating the symbiosis. This signal benefits both sender and receiver, allowing the fungi to colonize the root.	Some parasitic plants have evolved receptors to eves-drop on host strigolactones as a cue to sense host presence. The host plant does not benefit from sharing this information, and the cue only benefits the parasite receiver.

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Differences between signals and cues.
Source: Adapted from Ref. [19] with close-up of arbuscular mycorrhizal fungi connecting roots of plant hosts (photo credit: Y. Kobae) and parasitic plant *Striga gesnerioides* (photo: wiki commons).

Signals can be robust to some dishonesty, but this depends on the costs and benefits for the sender and receiver, and the reliability of the signal [22].

In contrast, cues rely on the eves-dropping of information and can lead to inadvertent communication (Figure 1). Cues benefit the receiver exclusively, with the receiver evolving to respond to their presence, much like a predator responds to the rustling sounds of unseen prey. For example, plants use cues, like airborne volatile organic compounds (VOCs), emitted from other plants to upregulate their own defenses [23]. The majority of these cases involve eves-dropping, although cases of cooperative signaling among plant kin have been demonstrated [24]. Some plants have evolved mechanisms to detect nanomolar concentrations of bacterial quorum sensing compounds produced by pathogenic and symbiotic partners [25]. Plants eavesdrop on quorum sensing compounds, using them as cues to upregulate responses, and even to stimulate the secretion of their own 'signal-mimic' substances to actively manipulate bacterial behaviors [25].

A long-standing hypothesis suggests that cues are precursors to signals [26]. Studying the evolutionary origins of signals helps us understand how microbes and plants may manipulate and co-opt molecules [27,28]. For example, endophytes in the genus *Colletotrichum* are generally pathogens, but the species *C. tofieldiae* is beneficial, providing phosphorus to hosts based on the hosts' phosphate starvation response [29]. This behavior, and the evolution from pathogenic to symbiotic lifestyle, likely evolved based on host cues, but now operates using interspecific signaling.

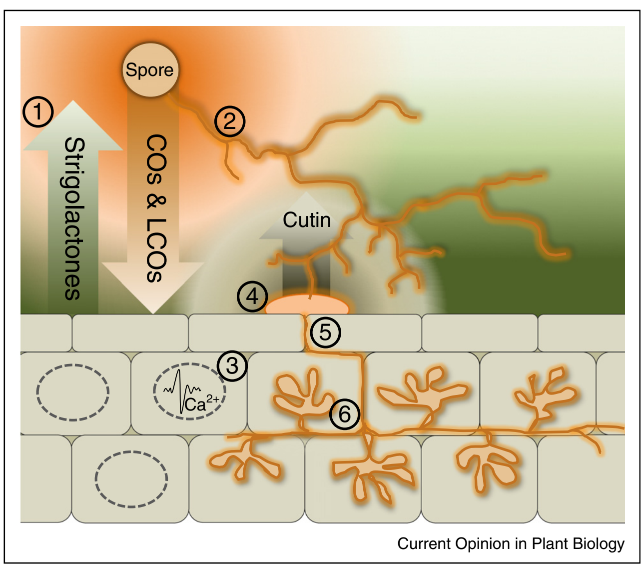
Extensive crosstalk between plant and fungi

Plants and microbes use signals to convey information about their environment and their readiness for colonization, but how can these reach the desired recipients, and not others [30]? Theoretically, effective communication is needed at two levels: (i) a wide screen, to distinguish among broad groups of microbes, stimulating mutualists rather than root-pathogens and (ii) a finer screen, to distinguish high and low-quality strains (from within a mutualist population) [31]. In the arbuscular mycorrhizal symbiosis, strigolactones (terpenoid lactones derived from the carotenoid metabolism) are key plant signaling molecules [20••]. While strigolactones are primarily plant hormones that regulate plant growth, their presence has been co-opted for the secondary function of attracting

AM fungi [reviewed in 32]. It has been hypothesized that initially mycorrhizal fungi relied on strigolactones as passive cues to indicate host presence, but host-derived compounds evolved into signaling molecules used to actively recruit mycorrhizal fungi [20••]. Strigolactones are defined as 'integrative signaling molecules' because they couple phosphorus availability (environmental signaling) with microbial recruitment (symbiosis signaling) to mediate architecture and productivity [33]. Strigolactones activate the metabolism of the AM fungus, promoting growth towards the roots (Figure 2) [34]. The strigolactone receptors of mycorrhizal fungi have yet to be discovered [35], but are likely different from plants, suggesting that they evolved independently and specifically to detect host presence [20••]. Strigolactones emitted by plants differ from host to host, and these profiles may help hosts attract certain fungal species or strains, but this is an open area of research [36•].

The current idea is that a host plant relies on the signaling molecules exuded by the AM fungi to prime itself for colonization (Figure 2), but also to distinguish mutualists and pathogens [20••]. However, as is expected in inter-species signaling systems, an evolutionary arms race exists, with parasites evolving ways to mimic cooperative signals. For example, recent work suggests that pathogenic oomycetes have recruited mycorrhizal signaling components,

Figure 2



Schematic overview of crosstalk between AM fungi and root required to form the symbiosis. (1) Root-derived strigolactones are sensed by a germinating AM fungal spore, which (2) exudes a series of signaling molecules such as lipochitooligosaccharides (LCOs) and chitooligosaccharides (COs). These molecules (3) trigger a series of reactions in the plant root: the cytosol calcium concentration increases, activating AM fungal induced gene expression, which leads to the formation of the pre-penetration apparatus. The reacting root will (4) secrete cutin monomers, signaling the fungi to form a (5) hypopodium and (6) initiate arbuscular growth [20••].

using cutin monomers as cues to recognize plant surfaces and promote infection structures [37].

While in the majority of cases, AM fungi and the host plants are both the senders and receivers of information, there are rare examples when this symmetry is skewed. AM fungi may use cues to initiate colonization and obtain resources from non-hosts, such as *Arabidopsis*, when their network is simultaneously supported by a host plant [38]. Fungal cues may also be used among AM fungi themselves. Because spores can germinate in the absence of hosts, they are likely triggered from fungal cues emanating from the hyphal network, such that hyphae from spores connect into larger compatible fungal networks (via anastomosis) [39]. Whether these are passive cues or active signals to recruit germinating spores require more research.

How parasitic and myco-heterotrophic plants use microbial signals as cues

Once signals are released into the rhizosphere, they become public goods. This means other organisms can eves-drop and use signals that are not directed at them, as cues. For example, strigolactones were first discovered in their capacity to attract parasitic plants of the genera *Striga* and *Orobanche* (Figure 1) [40]. Strigolactones are used by these parasites (which extract nutrients by penetrating host tissues) as a cue for host presence [36•,41]. Why plants would emit molecules that directly stimulate plants parasitizing them was an open question, but now this research has become a perfect illustration of how signals directed at symbiotic organisms are used as cues for parasitic organisms.

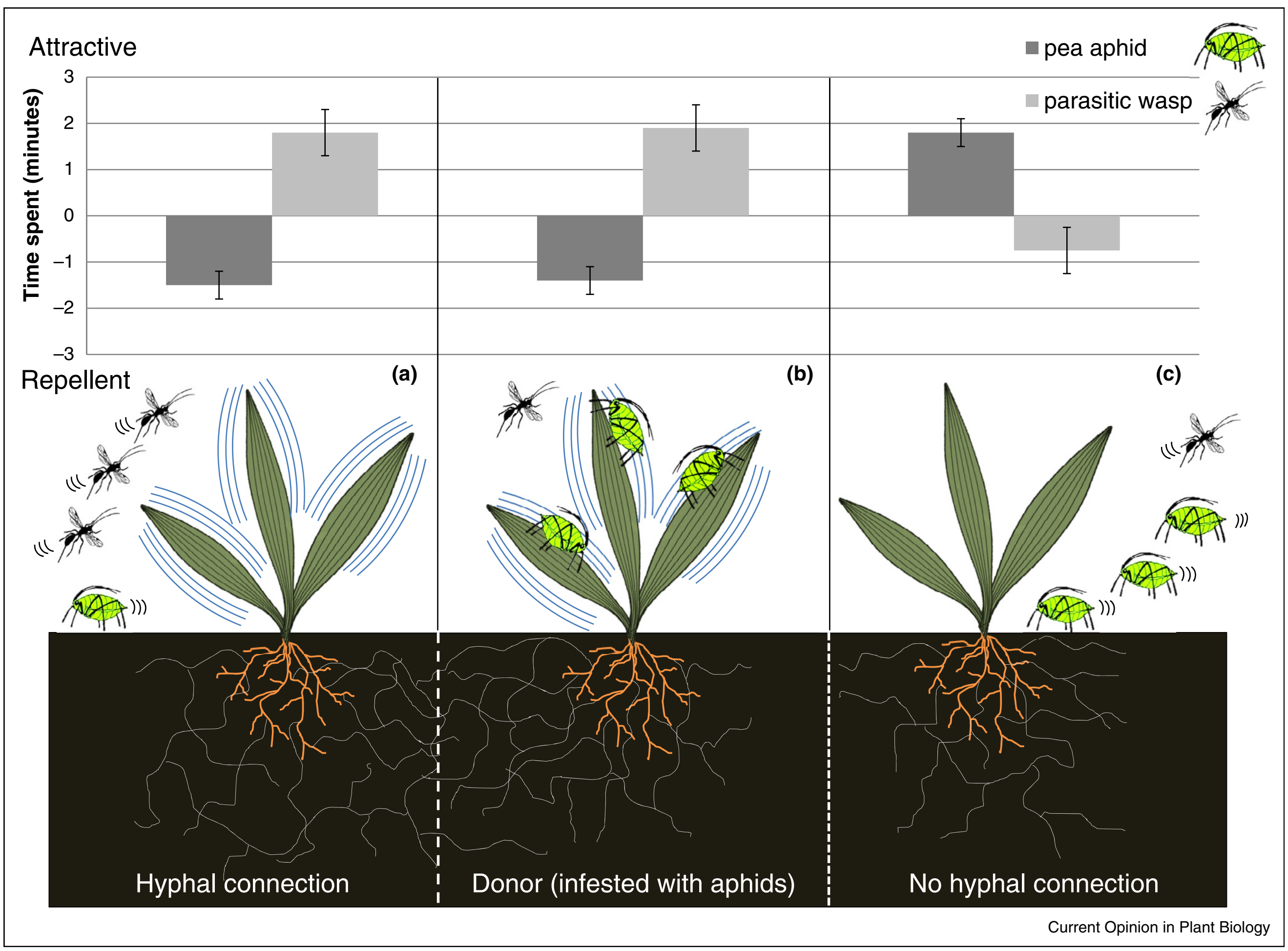
In other cases, parasitic plants use the fungal network itself to gain resources. Myco-heterotrophs are small (non-chlorophyllous) parasitic plants that tap directly into fungal networks, extracting carbon and nutrients [42]. While little is known about the chemical communication between myco-heterotrophs and AM fungi, seeds are thought to require some cue of fungal host presence for germination [43]. How have these myco-heterotrophs plants co-opted signaling molecules to tap undetected into the hyphal network, and what prevents this deceptive strategy from further spread [42]? One idea to explain their evolutionary persistence is that the cost of myco-heterotrophs and partial mycoheterophs (i.e. chlorophyllous at later development stages) on host plants is low [44], such that there is less selection against these parasites.

Plant–plant communication via common AM networks

Communication among plants may also be facilitated via underground fungal networks [45]. The induction of systematic changes in plant defenses in herbivore-free hosts when connected by a common mycorrhizal network to an herbivore-exposed host has been demonstrated; when the hyphal network was severed, no upregulation of the neighbor was found [21] (Figure 3). While these experiments, and others showing similar patterns [47•,48], are well-designed and robust, the use of the word 'signal' may be inappropriate, and researchers need to remain cautious in interrupting these results as being an adaptive 'warning system'. This is because it has yet to be convincingly demonstrated that the shared information results in a fitness benefit to both sender and receiver, and evolved to convey information about the signaler (Figure 1). The outstanding question is: what benefit does a sender plant gain from warning a competing neighbor against herbivores? Hypotheses have been put forward that the fungus benefits from the transfer of defense-related compounds, such that 'signals' are preferentially allocated to plants providing more carbon to the fungus [50], similar to the way nutrients are preferentially allocated [31]. However, this has been difficult to test because of issues in measuring fungal fitness and tracking defense compounds.

There is evidence of measurable benefits shared among plant kin (siblings compared to strangers) when incorporated in a common mycorrhizal network [51], and this type of kin selection can have clear evolutionary advantages. However, benefits to non-relatives [e.g. 46,48,52] are more likely explained by the fungal network acting as a conduit for chemical cues detected by other hosts. It is also possible that 'signaling plants' are favored by the network, since these plants may be providing more carbon (via 'signals') to the hyphae, thus creating a feedback

Figure 3



Plant–plant communication using common AM fungal networks. A donor plant **(b)** infested with aphids increases it defenses against the herbivores by emitting volatiles. These chemicals are repellent to pea aphids, and attract parasitic wasps that parasite on aphids. Plants connected via an underground hyphal connection **(a)** with these donor plants also increase their defenses. They then start to emit volatiles, which repel aphids and attract parasitic wasps. When there is no hyphal connection between plants **(c)** then plants do not upregulate their defenses and are still attractive to aphids.
Source: Adapted from Ref. [21].

loop [46]. To delineate a signal from a cue, more evidence is needed to accurately quantify costs and benefits, for example determining if compounds are expensive to produce [53], and if they move actively or passively. Until more experiments unequivocally show advantages gained by sender plants of 'signaling' to their neighbors, it is safer to use term 'infochemicals' as advocated by Barto *et al*. [54], a neutral term that does not specifying evolved benefits to senders and receivers.

Conclusion

While we continue to develop tools to decode the molecular basis of plant and microbial cross-talk, more attention needs to be paid to the evolutionary origins and exploitation of signals and cues [22]. In rhizosphere mutualisms, relatively robust mechanisms exist that allow hosts to broadly distinguish among pathogens and mutualists [20••]. However, we know little about the next level of specificity, namely how selection for quality (rather than just identity) can evolve [55]. In general, discriminating partners based on actual resources received, rather than signals, is evolutionarily more robust. Other possible solutions are to impose a cost, such that the host environment is toxic for organisms without the correct physiology, such as in the squid-light symbiotic organ (*Vibrio fischeri–Euprymna scolopes)* [56] or to directly couple the transfer of nutrients from one partner to the other [52]. As we understand more about these 'rules of engagement', we can begin to manipulate communication to our benefit, enhancing positive associations, and decreasing negative ones [27].

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