Social networking in crop plants: Wire and wireless cross-phytobiome communications

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Abstract

ants share the phytobiome with other members of the ecological community by sharing their physiology. The phytobiome is a collective ecological entity that senses external and internal stimuli via its member's sensing apparatus (senome). The activated senome generates intercellular, and intra- and inter-organismal signals that induce genetically and epigenetically dependent modifications of phytobiome member transcriptomes. Ultimately, these genetic modifications alter the phenotypes of the collective phytobiome members. Mycorrhiza, epiphytic fungi, and dodder can physically transfer signals between kin and non-kin plants. Phytobiome members can release infochemicals by themselves, or modify plant volatile emissions and root exudates to act as signals for plant–plant interactions. These signals can change plant physiology and induce holobiont updates in receiver plants via a facilitative or competitive mechanism. Receiver plants eavesdrop on phytobiome cues and signals to anticipate responses to unfolding challenges. An emerging body of information in plant–plant interactions through inter-kingdom communication can be exploited in integrated crop management under field conditions. However, a holistic view is crucial for the manipulation of complex systems, such as the phytobiome, to avoid potential butterfly effects.

1 ? INTRODUCTION

Humans have empathic perceptions so that if one member is afflicted with pain, other members will become uneasy (Saadi Shirazi, 1210-1292).

Plant seeds inherit information for their lifecycles directly from their parents, although much of the genomic information has been acquired from ancestors such as ferns, bryophytes, and Cyanobacteria (Sánchez-Baracaldo, Raven, Pisani & Knoll, 2017, Sharifi & Ryu, 2018c). Plants harbor genes and signaling pathways that function during symbiosis with Cyanobacteria and Lycophytes, which can be traced back to the origins of vascular plants (Jia, Kollner, Gershenzon & Chen, 2018, Sánchez-Baracaldo *et al.* , 2017, Sharifi & Ryu, 2018c). Symbiotic relationships have continuously developed during the co-evolution of plants and microbes, and include the exchange of genetic elements, signal molecules, and nutrients (Jia *et al.* , 2018, Papale, Saget & Bapteste, 2020, Sharifi & Ryu, 2018b).

Recent reports proposed that multicellular organisms (e.g., animals and plants) and their associated unicellular organisms (e.g., microbes) could be considered as super-organisms, or holobionts (in ancient Greek, holos means whole and biont means unit of life) (Gilbert, 2019, Suarez & Stencel, 2020). However, the definition and concept of a holobiont is still debated. We consider a holobiont as an ecological unit (assembly) of a group of organisms that gather together based on their evolutionary capability to achieve a common purpose, which is survival of the holobiont. A holobiont undergoes natural selection as a team or assembly (Gilbert, 2019, Osmanovic, Kessler, Rabin & Soen, 2018). Members of the holobiont retain their individuality during symbiosis, but share their genetics and physiological capabilities to sustain the holobiont. The introduction and persistence of members in the holobiont is modulated by individual signaling pathways and

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innate immunity systems, especially for core animal and plant members (Carrión, Perez-Jaramillo, Cordovez, Tracanna, de Hollander, Ruiz-Buck, Mendes, van Ijcken, Medema & Raaijmakers, 2019, Carvalhais, Dennis, Badri, Kidd, Vivanco & Schenk, 2015, Cotton, Petriacq, Cameron, Meselmani, Schwarzenbacher, Rolfe & Ton, 2019, Korenblum, Dong, Szymanski, Panda, Jozwiak, Massalha, Meir, Rogachev & Aharoni, 2020, Mannaa, Han, Jeon, Kim, Kim, Park, Kim & Seo, 2020). The holobiome includes all living organisms, their genetic materials, and their primary and secondary metabolites and molecules produced within a particular habitat (Berg, Rybakova, Fischer, Cernava, Vergès, Charles, Chen, Cocolin, Eversole & Corral, 2020, Sharifi & Ryu, 2017).

The microbiome includes the microbial community living in a particular habitat and their metabolites, mobile genetic elements, and relic DNA (Berg *et al.*, 2020). The microbiome helps the holobiont survive during biotic and abiotic stresses. The presence and abundance of specific microbial species in the microbiome change during successive phases of plant ontogeny and during biotic/abiotic stresses (Carrión *et al.*, 2019, Cotton *et al.*, 2019, Edwards, Santos-Medellın, Liechty, Nguyen, Lurie & Eason, 2018, Gu, Wei, Wang, Friman, Huang, Wang, Mei, Xu, Shen & Jousset, 2016). The rice microbiome changes gradually during plant development: change is dynamic during the vegetative stage but more stable during the reproductive stage (Edwards *et al.*, 2018). Biotic and abiotic stresses modulate the plant microbiome toward plant defense responses or plant tolerance (Cotton *et al.*, 2019, Dini-Andreote, 2020, Gu *et al.*, 2016). For example, *Flavobacteriaceae* and *Chitinophagaceae* populations increase in the endosphere of sugar beet infected with *Rhizoctonia solani* in suppressive soil. These bacteria produce chitinase and other cell wall degradation enzymes to suppress the pathogen (Carrión *et al.*, 2019).

Plants continuously perceive and generate signals resulting from interactions between plant cells and the microbiome to encounter biotic/abiotic stresses that could reduce performance or threaten survival, although the microbial members of the holobiont promote plant health (Erb, Veyrat, Robert, Xu, Frey, Ton & Turlings, 2015, Sharifi & Ryu, 2018c). Plants adapt to stress via sensor elicitation, signaling cascade activation, gene expression, and phenotype modification (Glazebrook, 2005, Jung, Tschaplinski, Wang, Glazebrook & Greenberg, 2009). Signal processing time is critical for success or failure in stress responses. Plants acquired the ability to anticipate and respond to imminent dangers, which conferred ecological competence in highly dynamic ecosystems. This system is known as defense priming (Conrath, Beckers, Langenbach & Jaskiewicz, 2015, Jung *et al.*, 2009). Plants can acquire early warning information through their microbiome and plant–plant signals (Gilbert & Johnson, 2017, Vahabi, Reichelt, Scholz, Furch, Matsuo, Johnson, Sherameti, Gershenzon & Oelmuller, 2018, Yi, Heil, Adame-Alvarez, Ballhorn & Ryu, 2009). The plant microbiome (phytobiome) can exploit the unique capabilities of each of its members for the benefit of all members, including the mycorrhizal network, dodder, and endophytic fungi, which directly prime plant defense responses or transfer inter-plant signals (da Trindade, Almeida, Xavier, Lins, Andrade, Maia, Mello, Setzer, Ramos & da Silva, 2019, Hettenhausen, Li, Zhuang, Sun, Xu, Qi, Zhang, Lei, Qin, Sun, Wang, Baldwin & Wu, 2017, Vahabi *et al.*, 2018). The plant microbiome and macrobiome, including parasitic plant dodder and insect pests, can modify plant-derived inter-plant signals such as volatiles and root exudates (Figure 1) (Sharifi, Lee & Ryu, 2018, Song, Sim, Kim & Ryu, 2016). Herbivore-induced plant volatiles (HIPVs) and microbe-induced plant volatiles (MIPVs) are good examples of inter-plant signals (Heil & Bueno, 2014, Sharifi *et al.*, 2018).

Here, we review microbe-mediated and plant-mediated plant–plant communications that improve plant defense against pathogenic microbes. From multiple layers of plant–plant communications, we distinguished two distinct types: wired and wireless communications. Wired communication involves one plant sending a signal to another plant though direct contact via microbial structures and hyper-parasitic plant organs. This can be considered as an information highway mediating plant–plant communication. Wireless communication involves signal transfer across the space separating two plants. We investigated how wired and wireless communications affect plant defense responses. We determined that these signal transduction pathways proceeded via the following three steps: signal input (extracellular signal perception generates an endogenous signal cascade); transferring signal (direct connection from signal producer to receiver through mycorrhizal network and parasitic plants, and indirect signal translocation via plant volatile compounds and exudates); and signal output (receiver plant responses to biotic and abiotic stresses).

2 ? WIRED COMMUNICATION

2.1 ? Wired connections between clonal plants via rhizomes and stolons

Some plants produce genetically identical but independent plants (clones) through specific organs such as rhizome and stolon (Bittebiere, Benot & Mony, 2020, Vannier, Mony, Bittebiere, Theis, Rosenberg & Vandenkoornhuyse, 2019). These clonal plants are two functionally independent plants that share vascular connections and physiological integration. Clones have similar microbiomes, and represent unique models in plant–plant interaction studies (Vannier *et al.* , 2019). Clones communicate and enhance each other's survival during biotic/abiotic stress (Karban, Wetzel, Shiojiri, Ishizaki, Ramirez & Blande, 2014, Qian, Li, Han & Sun, 2010, Semchenko, John & Hutchings, 2007). The organ connecting clonal plants can be severed via natural or artificial methods to generate two physically separated plants, which become alienated with time (Chen, During & Anten, 2012). Second- and third-order clones (ramets) display higher competition with the first ramet after severing (Karban & Shiojiri, 2009). Physical connections via stolon and rhizome can mitigate abiotic stress by transferring/exchanging nutrients and metabolites, or by modulating resource use efficiency (Figure 1) (Roiloa, Antelo & Retuerto, 2014). Defense signals can be transferred via phloem from older to younger ramets to induce systemic resistance in young ramets. Older ramets do not receive defense signals from younger clones due to the direction of source-sink gradient flow (Gomez & Stuefer, 2006). In *Trifolium repens* , a defense signal against *Mamestra brassicae* larvae can be transferred to younger ramets within 35–51 h depending genotypic variation. Induced but undamaged ramets lost their resistance after 28 days (Gomez, Van Dijk & Stuefer, 2010).Besides direct linked plant-plant via plant part, the higher parasitic plants also have an important role in wired communication to enhance plant fitness.

2.2 ? Wired connections between independent plants via Dodder-mediated interspecific signaling

Dodder is a plant holoparasite that acquires water and nutrients from host plants via the haustorium, which physically connects the parasite to its host. Dodder species have broad host range, and can interconnect several plant species or clusters of the same species (Figure 1) to generate a common dodder network. The common dodder network can be considered as an inter-plant highway that translocates large numbers of proteins, RNA, metabolites, and plant viruses over a distance of at least 100 cm (Hettenhausen *et al.* , 2017, Zhuang, Li, Song, Hettenhausen, Schuman, Sun, Zhang, Li, Song & Wu, 2018). The common dodder network can translocate more than 1,500 proteins between soybean and Arabidopsis, and some of these proteins can localize in dodder seeds. Approximately 15–30% of dodder proteins have host origin, including transcription factors and R proteins that may function in signal transaction. Dodder proteins can transfer to host plant cells. Plants can anticipate future threats by receiving neighboring plant signals transferred through the common dodder network. Although there are few reports on the role of the common dodder network in inter-plant signaling, the results indicate that these transferred signals are important in biotic/abiotic stress responses. When a host of dodder plant is under abiotic stress such high salinity, dodder transfers salinity stress signals through a cluster of plants at a rate of 1.2 cm per min, which prime salt tolerance in neighboring receiver plants. This receiver plant priming changes the transcriptome, proline levels, and stomatal conduction, so that the receiver plant stress response becomes similar to that of the donor plant (Li, Zhang, Liu, Liu, Shen, Zhuang & Wu, 2020).

Plants infected with different herbivorous insects transfer relatively long-distance signals to conspecific and heterospecific neighbors via the common dodder network (Hettenhausen *et al.* , 2017, Zhuang*et al.* , 2018). *Myzus persica* infestation reduces the contents of salicylic acid (SA) and jasmonic acid (JA) in dodder by up to 58% and 41%, respectively. Aphids can modulate hormonal signaling by injecting effector proteins into dodder plants (Rodriguez & Bos, 2013). Aphid-infested dodder induce JA but not SA in soybean hosts, and subsequent phloem sap feeding by *M. persica* and chewing by*Spodoptera litura* causes 41% and 20% less damage, respectively, in dodder-infected plants than in control plants. Dodder transfers signals from insect-damaged soybean to conspecific or heterospecific plants, such as tomato and Arabidopsis. Gene expression and RNA-seq analyses reveal intense transcriptome modification in receiver plants. An unknown signal can translocate between common dodder network–connected Arabidopsis plants at a rate of 1 cm/min. A wave

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of signal transduction propagated between connected Arabidopsis plants, as intracellular WRKY 40 and WRKY53 transcription factors reached maximum expression at 45 and 90 min after donor plant damage in the second and fourth plants in the cluster, respectively (Zhuang *et al.* , 2018).

2.3 ? Wired connections between plants via fungal hyphae of the mycorrhizal or endophytic fungal network

Fungi can act as messengers to transfer information between independent plants. Plant-mycorrhiza symbiosis is an ancient system that arose more than 450 million years ago (Waters, Gutjahr, Bennett & Nelson, 2017). This symbiosis had a crucial role in land colonization by plants. Different fungal phyla have evolved different types of plant-mycorrhiza symbiosis. Arbuscular mycorrhizae (AM) fungi belong to Glomeromycota, and establish symbiotic relationships with 78% of plants, especially in grassland, tropical rainforest, and agricultural fields (Tedersoo, Bahram & Zobel, 2020). Ectomycorrhiza (EcM) belong to several fungal phyla, and establish symbiotic relationships with 2% of plants, especially in temperate and coniferous forests (Pickles, Wilhelm, Asay, Hahn, Simard & Mohn, 2017, Tedersoo *et al.* , 2020). EcM form a rhizomorph structure that can spread over several meters. There are two further types of symbiotic mycorrhiza: ericoid and orchid. Ericoid mycorrhiza belong to Phallales, Boletales, and Russulales orders of Basidiomycota, and establish symbiotic relationships with 400 plant species from the Monotropoideae subfamily of Ericaceae. These plants do not have chlorophyll and obtain 85–100% of required carbon from fungi, which are simultaneously connected to autotroph nurse trees (Min, Chang-Qin, Yong-Peng, Welti, Moreau & Selosse, 2012, Simard, 2018). Some *Brassicaceae* and *Proteaceae* plants do not participate in mycorrhizal relationships, and are considered to be non-mycorrhizal symbiotic plants (Tedersoo *et al.* , 2020). These plants can interfere in the mycorrhizal establishment of other plants (Cipollini, Rigsby & Barto, 2012). For example, *Alliaria petiolata* produces glucosinolate-derived exudate that suppresses the mycorrhizae of neighboring plants (Cipollini *et al.* , 2012).

Mycorrhizae have important roles in inter-plant nutrient transfer (especially carbon, phosphorus, and nitrogen), allelochemicals, and signal molecules. Mycorrhizae are common in soil, as 1 g of soil contains 10–100 meters of mycorrhizal fungi (Gilbert & Johnson, 2017). These fungi have broad host ranges and can connect several plants from different taxa. Closely-related mycorrhiza fungi can perform anastomosis to generate a network (Figure 1), which is called a common mycorrhiza network (Deja-Sikora, Mercy, Baum & Hrynkiewicz, 2019). Some plant species exploit the common mycorrhiza network, especially EcM, to transfer nutrients and signals and promote the establishment and survival of conspecific seedlings. Mycorrhiza colonization affects community structure and dominance of specific plant species in natural ecosystems (Bennett, Cahill & van der Heijden, 2016, Hortal, Lozano, Bastida, Armas, Moreno, Garcia & Pugnaire, 2017). EcM support their plant partner by transferring large amounts of organic carbon, changing the hyphosphere microbiome, and directly or indirectly suppressing plant pathogens (Chen *et al.* , 2012, Liang, Johnson, Burslem, Yu, Fang, Taylor, Taylor, Helgason & Liu, 2020, Pickles *et al.* , 2017). A comprehensive study performed over 10 years in 1200 plots in a Chinese forest reported that EcM acts as a mediator in supporting the establishment and survival of young plants by adult nurse conspecifics. Inhibiting the EcM connection between plants using a 0.5-μm mesh markedly reduced seedling survival. The abundance of plant pathogenic fungi also decreased in EcM-colonized plots (Liang *et al.* , 2020).

Plants exploit mycorrhizae fungi for long-distance transfer of plant signals and allelochemicals. *Tagetes tenuifolia* secrete the lipophilic allelopatic compound thiophenes and the hydrophilic allelopatic compound imazamox, which diffuse more than 12 cm via the common mycorrhiza network (Barto, Hilker, Muller, Mohney, Weidenhamer & Rillig, 2011). Mycorrhizae fungi can translocate defense signals to neighboring unstressed plants, similarly as dodder. Tomato plants infected with the nectrotrophic pathogenic fungus *Alternaria solani* transfer a signal to non-infected neighbors at 18 h post-inoculation via mycorrhizae hypha. In those receiver plants, the relative expression levels of defense-related genes such as phenylalanine ammonialyase (PAL), lipoxygenase, polyphenol oxidase, and pathogenesis-related proteins (PR1, PR2, and PR4) were the same as those in the donor plants (Song, Zeng, Xu, Li, Shen & Yihdego, 2010). Signal transduction via the common mycorrhiza network also has been detected for herbivore-damaged plants (Babikova, Gilbert,

Bruce, Birkett, Caulfield, Woodcock, Pickett & Johnson, 2013, Song, Ye, Li, He, Zhu-Salzman, Wang, Su, Luo & Zeng, 2014).

Stressed plants can recruit mycorrhizae by regulating strigolactone signaling. Plant strigolactones are multifunctional hormones with pivotal roles in plant ecological relationships: strigolactones promote mycorrhiza spore germination and hyphal branching (Waters *et al.* , 2017); modify fungal and bacterial populations including those of plant pathogens in the rhizosphere (Carvalhais, Rincon-Florez, Brewer, Beveridge, Dennis & Schenk, 2019, Liu, Rice, Lopes, Grewal, Lebeis, Hewezi & Staton, 2020); establish cross-talk with defense-related hormones such as JA, SA, and ABA; and modulate plant resistance to different plant pathogenic fungi and bacteria (Lopez-Raez, Shirasu & Foo, 2017). Pathogen infection can induce plants to modulate strigolactones biosynthesis to recruit mycorrhiza and other beneficial microbes.

Fungal signal transduction is not exclusive to mycorrhizae. Other mutual and pathogenic fungi with long-term endophytic relationships with plants have the potential to transfer signals between plants. Some soil fungi can serve as a bridge between host plants. For example,*Piriformospora indica* transfers signals from infected*Arabidopsis* to neighboring *Arabidopsis* plants.*Alternaria brassicae* activates JA pathways in infected focal plants. By contrast, endophytic fungi convert a specific JA signal to generate an ABA signal in neighboring (receiver) plants (Vahabi *et al.* , 2018).

Fungi serve as vectors for the transfer of plant viruses among plants. Although plants and fungi are not phylogenetically related, they can be infected by phylogenetically-related viruses (Roossinck, 2019). Some plant viruses propagate in the fungal cytosol and transfer between host plants based on the host range of both fungi and viruses. A virus from the saprophytic endophyte *Penicillium aurantiogriseum* replicates in the host plant (Nerva, Varese, Falk & Turina, 2017). *Cucumber mosaic virus* is a broad-range virus that can survive in the pathogenic fungus *Rhizoctonia solani* , which has a broad host range. *R. solani* transfers this virus to a neighboring host (Andika, Wei, Cao, Salaipeth, Kondo & Sun, 2017). There is evidence that plant virus enters fungal spores and achieves long-distance dissemination via wind dispersal of the fungal spores. *Cryphonectria* transfer*Cryphonectria hypovirus 1* to tobacco, which subsequently propagates and spreads systemically throughout the plant with the help of *Tobacco mosaic virus* (TMV) movement protein. TMV also enters fungi and propagates with the help of *Cryphonectria hypovirus 1* , which can spread to other hosts via fungal spores (Bian, Andika, Pang, Lian, Wei, Niu, Wu, Kondo, Liu & Sun, 2020).

3 ? WIRELESS COMMUNICATION: SIGNAL INPUT-TRANSFER-OUTPUT MODEL

Plants normally release volatile and non-volatile chemicals that can be exploited by other plants as a source of signal molecules (infochemicals). Here, we discuss how these plant infochemicals can be modulated by microbes, insects, and environmental stimuli. These infochemicals diffuse via air and soil pores to reach neighbor plants. Receiver plants can amplify the released infochemical signals to expand the effective infochemical signaling zone. Infochemicals perceived by the receiver plants can act as kin recognition signals, growth inhibitors (allelopathy), growth stimulators, and defense signals (Karban, Shiojiri, Ishizaki, Wetzel & Evans, 2013, Kong, Zhang, Li, Xia, Yang, Meiners & Wang, 2018, Sharifi *et al.* , 2018, Sharifi & Ryu, 2018b). Infochemicals can directly change the transcriptome and physiology of receiver plants to prime for imminent threats, or they may indirectly change the plant microbiome in neighboring plants through a facilitative or competitive mechanism (Carvalhais *et al.* , 2015, Mannaa *et al.* , 2020, Vannier, Bittebiere, Mony & Vandenkoornhuyse, 2020).

3.1 ? Wireless signal input

3.1.1 ? Constitutive release of infochemicals as information sources

Plants continuously release a profile of volatile organic compounds (VOCs) and non-VOCs to the root and atmosphere (Table 1). These chemical profiles, concentrations, and release time courses function as signals of plant presence and health status. Constitutive release of specific chemical signatures can be exploited by neighbor organisms to determine the presence and identity of neighboring plants. Receiver plants recognize the degree of phylogenetical relationship of neighbor plants to discriminate kin and non-kin

plants (Delory, Delaplace, Fauconnier & du Jardin, 2016, Palmer, Ali, Yang, Parchami, Bento, Mazzella, Oni, Riley, Schneider & Massa, 2016). Chemicals such as ethylene released from healthy plants are sensed by insects, parasitic plants, and neighboring plants as a cue to change their behavior (Pierik, Visser, de Kroon & Voesenek, 2003, Robert, Erb, Duployer, Zwahlen, Doyen & Turlings, 2012, Runyon, Mescher & De Moraes, 2010). For example, exposing potato to healthy onion changes potato volatiles, which are repellent to an aphid pest and attractive to the aphid predator ladybird beetle (Ninkovic, Dahlin, Vucetic, Petrovic-Obradovic, Glinwood & Webster, 2013, Vucetic, Dahlin, Petrovic-Obradovic, Glinwood, Webster & Ninkovic, 2014). (E)-nerolidol and ($3E$,$7E$)-4,8,12-trimethyl-1,3,7,11-tridecatetraene were the primary effective volatiles released by exposed potato plants (Vucetic *et al.*, 2014). In most cases, signals from healthy plants can affect neighboring plants by modifying biomass allocation, lateral root formation, and chlorophyll and phenolic compound biosynthesis, or directly inhibiting seed germination (Delory *et al.*, 2016, Takigahira & Yamawo, 2019). The sagebrush volatile compounds methyl jasmonate, camphor, 1,8-cineol, α-thujone, and nerol inhibit the germination of *Nicotiana attenuate* seeds (Jassbi, Zamanizadehnajari & Baldwin, 2010).

Some plant infochemicals are released primarily by healthy plants and can be considered as a marker of plant health status. Isoprene emission levels are linked to plant health and photosynthetic efficiency. The reduction of isoprene emission after pest and disease attacks is considered as a marker for plant stress (Copolovici, Kannaste, Pazouki & Niinemets, 2012, Jiang, Ye, Veromann & Niinemets, 2016, Toome, Randjärv, Copolovici, Niinemets, Heinsoo & Luik, 2010). Isoprene alleviates plant oxidative stress (van Doorn, Merl-Pham, Ghirardo, Fink, Polle, Schnitzler & Rosenkranz, 2020). Neighboring plants can decode the information signals contained in the time course of VOC emission, spatiotemporal chemical stability, location of emission, and emission quantity (Erb *et al.*, 2015, Jiang *et al.*, 2016, Piesik, Pańka, Jeske, Wenda-Piesik, Delaney & Weaver, 2013).

3.1.2 ? Microbes and insects induce the emission of specific plant volatiles

Microbes and insects modulate plant volatile emission dynamics by decreasing some VOCs and increasing others, or by inducing *de novo* VOC synthesis (Table 1). Plant volatiles are produced by several metabolic pathways, including plastidic methylerythritol phosphate and cytosolic mevalonic acid pathways (terpenoid compounds), shikimic acid pathways (benzoid and phenylpropanoid compounds), and oxylipin pathways [green leaf volatiles (GLVs)] (Bouwmeester, Schuurink, Bleeker & Schiestl, 2019). The emitted VOC profile is related to the plant genotype, organ, and type of biotic/abiotic trigger. Different comparative triggers (e.g., chewing vs. sucking/piercing, biotroph vs. necrotroph, host vs. non-host pathogens, and saprophytic beneficial vs. parasitic pathogenic microbes) elicit distinct bouquets of VOCs, including the quantity and quality of each compound and its emission time course (Castelyn, Appelgryn, Mafa, Pretorius & Visser, 2014, Klimm, Weinhold & Volf, 2020, Qawasmeh, Raman & Wheatley, 2015, Quintana-Rodriguez, Morales-Vargas, Molina-Torres, Ádame-Alvarez, Acosta-Gallegos, Heil & Flynn, 2015, Sharifi *et al.*, 2018). VOC profiles are conventionally defined based on the triggers, including HIPVs, oviposition-induced plant volatiles, MIPVs, and stress-induced plant volatiles (Kessler & Heil, 2011, Sharifi *et al.*, 2018). These categories normally contain all of the above-mentioned VOC groups, but the quantity/quality and emission time course for each compound carries specific information. GLVs are categorized as HIPVs, especially for chewing insects, but GLVs also are emitted from microbial pathogen-infected plants (Ameye, Allmann, Verwaeren, Smagghe, Haesaert, Schuurink & Audenaert, 2018). Rust disease disrupts the epidermis and induces the release of high amounts of GLVs (Jiang *et al.*, 2016). By contrast, chewing insects feeding on maize root did not elicit the emission of GLVs, and maize root did not respond to GLVs (van Doan, Züst, Maurer, Zhang, Machado, Mateo, Ye, Schimmel, Glauser & Robert, 2020).

Plants emit VOCs in response to signaling between plants and Invaders. Plant VOC profiles were altered by pathogen-associated molecular patterns (PAMPs), herbivore-associated molecular patterns (HAMPs), damage-associated molecular patterns (DAMPs), effector proteins, and microbial volatile compounds (Figure 2) (Ameye *et al.*, 2018, Bouwmeester *et al.*, 2019, Rybakova, Rack-Wetzlinger, Cernava, Schaefer, Schmuck & Berg, 2017, Sharifi *et al.*, 2018, Wu, Qi, Li, Tian, Gao, Wang, Ge, Yao, Ren, Wang, Liu, Kang, Ding & Xie,

2017). These elicitors activate defense-related hormones (e.g., JA, SA, and their cross-talk), which in turn activate metabolic pathways that produce the main VOC groups. HAMPs such as volicitin, caeliferins, and β-glucosidase modify the volatile profiles in several plants (Alborn, Turlings, Jones, Stenhagen, Loughrin & Tumlinson, 1997, Alborn, Hansen, Jones, Bennett, Tumlinson, Schmelz & Teal, 2007, Hopke, Donath, Blechert & Boland, 1994). These compounds can induce or suppress specific groups of volatiles to attract or repel parasitoids to host plants. Well-adapted maize caterpillars (*Spodoptera frugiperda*) suppress HIPVs in maize, but not in cotton (De Lange, Laplanche, Guo, Xu, Vlimant, Erb, Ton & Turlings, 2020). In some plant pathogens, PAMPs (e.g., flg22, laminarin, and glucan) and effector proteins (e.g., 2b) can modify plant VOCs (Chalal, Winkler, Gourrat, Trouvelot, Adrian, Schnitzler, Jamois & Daire, 2015, Leitner, Kaiser, Rasmussen, Driguez, Boland & Mithöfer, 2008, Sobhy, Bruce & Turlings, 2018, Tu, Yang, Xu, Chen, Luo, Zhu, Chen & Yan, 2017, Tungadi, Groen, Murphy, Pate, Iqbal, Bruce, Cunniffe & Carr, 2017). PAMPs, HAMPs, and effector proteins are perceived by pattern recognition receptors and R proteins in plants, and subsequently activate basal and effector-triggered plant immune responses (Bonaventure, VanDoorn & Baldwin, 2011, Glazebrook, 2005).

Insertion of single R protein and its position in the genome can significantly change the emission of volatiles (Figure 2) (Lazebnik, Tibboel, Dicke & van Loon, 2017). Subsequent signaling pathways (e.g., SA- and JA-dependent pathways) leading to systemic resistance in inoculated and neighboring plants have important roles in volatile biosynthesis (Orlovskis & Reymond, 2020, Wenig, Ghirardo, Sales, Pabst, Breitenbach, Antritter, Weber, Lange, Lenk, Cameron, Schnitzler & Vlot, 2019). ENHANCED DISEASE SUSCEPTIBILITY1 (EDS1) and AvrRpm1 are essential factors in systemic acquired resistance and important regulators of VOCs synthesis in Arabidopsis (Bichlmeier, 2017). Monoterpenes such as α- and β-pinene also induce systemic resistance through EDS1, SA INDUCTION–DEFICIENT 2 (SID2), and NONEXPRESSOR OF PR GENES 1 (NPR1) proteins (Figure 3) (Bichlmeier, 2017). Thus, any biological and chemical modulator of plant resistance can change the VOC profile or prime VOC release in response to stress. *Pseudomonas protegens*strain CHA0 did not change β-caryophyllene emission or expression of the β-caryophyllene synthase gene, but primed them in response to maize beetle *Diabrotica balteata* (Chiriboga, Guo, Campos-Herrera, Röder, Imperiali, Keel, Maurhofer & Turlings, 2018). Bacterial pathogens *Pseudomonas syringae* directly induce the emission of 1-undecanol and (*Z*)-3-hexenol volatiles in common bean, which repel spider mite (*Tetranychus urticae*) (Karamanoli, Kokalas, Koveos, Junker & Farré-Armengol, 2020). Thus, signal cross-talk during simultaneous plant infestation with herbivores and pathogens (Eberl, Hammerbacher, Gershenzon & Unsicker, 2018, Lazebnik *et al.*, 2017, Peñaflor & Bento, 2019) or co-infestation with two pests (Kroes, Weldegergis, Cappai, Dicke & van Loon, 2017, Zhang, Broekgaarden, Zheng, Snoeren, van Loon, Gols & Dicke, 2013) can modulate VOC emissions and attract pests and their parasitoids.

3.2 ? Wireless signal transfer

Plant infochemicals can diffuse around the elicited plant (producer), and are amplified by receiver plants to expand their effective zone. Infochemicals can diffuse distances of a few centimeters to several meters according to their chemical structure and vectors such as mycorrhiza and dodder. Wheat infected by *Fusarium culmorum*transfers signals to neighbor plants located 1–3 meters distant. However, there is a negative correlation between distance and response intensity in the receiver plant. Several studies show that receiver plants also propagate signals and act as nodes in inter-plant signaling (Chen, Yang, Chen, Luo, Cui, Yan & Gerwick, 2019a, Piesik *et al.*, 2013, Wenig *et al.*, 2019). Thus, neighboring plants amplify signals in clusters of receiver plants. However, the regulation of induced signaling pathways involved in infochemical synthesis in receiver plants requires time, which results in a wave of infochemical synthesis and metabolic responses in receiver plants. Falik, Mordoch, Ben-Natan, Vanunu, Goldstein and Novoplansky (2012) observed that osmotic stress in *Pisum sativum* activated stomatal closure in the focal plant and the next three plants in the cluster within 1 h, whereas more distant plants responded after 1 h. In this study, focal plant stomata remained closed for 24 h, whereas receiver plants opened their stomatal apertures because they did not directly encounter osmotic stress. Receiver plants did prepare for imminent osmotic stress, with the ability to return to a naive state if the stress was resolved. Weed plants use stress signals from *P. sativum* neighbors to improve their acclimation (Falik *et al.*, 2012). (Wenig *et al.*, 2019) showed that monoterpenes such as

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α- and β-pinene act as immunity-inducing signals between plants (Figure 3). Systemic acquired resistance (SAR) is an SA-mediated induced resistance in systemic plant tissues that is effective against a broad range of plant pathogens (Wenig *et al.* , 2019). LEGUME LECTIN-LIKE PROTEIN1 (LLP1) is a predicted lectin that acts in the recognition of SAR signals, which also regulate intra- and inter-plant monoterpene synthesis. In the non-vascular marine alga *Pyropia haitanensis* , the 1-octone-3-ol plant–plant defense signal can self-stimulate in receiver plants and activate SA hormones (Chen *et al.* , 2019a).

3.3 ? Wireless signal output: Receiver plant response to biotic/abiotic stresses

The transferred signal is perceived by neighboring (receiver) plants and augments biotic/abiotic stress resistance responses (Table 1). VOC-mediated plant stress responses have been demonstrated in numerous studies, although the ethylene receptor ETR1 is the only plant VOC receptor identified to date (Chang, Kwok, Bleecker & Meyerowitz, 1993). Future research may discover additional receptors to plant VOCs. Recent studies identified different mechanisms whereby receiver plants perceive VOCs from neighbor plants. VOCs can be absorbed by a wax layer on the epidermal cell, which traps VOCs and slowly releases them to attract or repel herbivores and their parasitoids and entomopathogens (Camacho-Coronel, Molina-Torres & Heil, 2020, Lin, Hussain, Avery, Qasim, Fang & Wang, 2016). Some trapped volatiles such as methyl salicylate (MeSA), MeJA, and indole can be converted to the active plant hormones SA, JA, and indole-3-acetic acid (IAA), respectively (Figure 2,3) (Bailly, Groenhagen, Schulz, Geisler, Eberl & Weisskopf, 2014, Rivas-San Vicente & Plasencia, 2011). Some enzymes metabolize trapped volatiles such as (*Z*)-3-hexenol to the more active derivative (*Z*)-3-hexenylvicianoside (Sugimoto, Matsui, Iijima, Akakabe, Muramoto, Ozawa, Uefune, Sasaki, Alamgir & Akitake, 2014). Some GLVs induce plasma membrane potential depolarization in receiver plants, thereby activating reactive oxygen species (ROS) and calcium signaling (Figure 2) (Zebelo, Matsui, Ozawa & Maffei, 2012).

The perception of VOCs modifies the transcriptome, proteome, and metabolome in receiver plants (Kwon, Ryu, Lee, Park, Han, Lee, Lee, Chung, Jeong, Kim & Bae, 2010, van Dam & Bouwmeester, 2016, Zhang, Kim, Krishnamachari, Payton, Sun, Grimson, Farag, Ryu, Allen, Melo & Pare, 2007). In some cases, VOCs do not significantly change gene expression profiles and metabolic activity, but prime the plant to respond more rapidly and robustly to upcoming threats (Paschold, Halitschke & Baldwin, 2006, Quintana-Rodriguez *et al.* , 2015). Plant volatile (*Z*)-3-hexenyl acetate directly induces JA- and abscisic acid–related gene expression, whereas indole primes these genes in maize against *Spodoptera littoralis* (Hu, Ye & Erb, 2019). Several studies report that primed plants activate defense-related pathways based on the attacker identity rather than the inducer (Moreira, Nell, Katsanis, Rasmann & Mooney, 2018, Sharifi & Ryu, 2017). For example, VOCs from plants infested with general or specialized herbivores activate similar defense pathways and VOC emission profiles in healthy neighbors. By contrast, primed receiver plants mount a specific set of defense mechanisms based on the type of attacker (Moreira *et al.* , 2018). Infochemicals from neighbor plants can activate master regulatory systems involved in plant innate immunity, including leucine-rich repeat-receptor-like kinase, mitogen-activated protein kinases, WRKY transcription factors, and systemic acquired resistance (Figure 2, 3) (Dombrowski, Kronmiller, Hollenbeck, Rhodes, Henning & Martin, 2019, Dombrowski & Martin, 2018, Lee, Kim, Lee, Ahn & Ryu, 2020, Mirabella, Rauwerda, Allmann, Scala, Spyropoulou, Vries, Boersma, Breit, Haring & Schuurink, 2015, Wenig*et al.* , 2019, Ye, Glauser, Lou, Erb & Hu, 2019). D-Lactic acid secreted by the microalga *Chlorella fusca* primed defense in*Arabidopsis thaliana* against *Pseudomonas syringae* pv. tomato DC3000 by increasing the expression of WRKY transcription factors and cysteine-rich receptor-like kinases, and induced both SA- and JA-dependent pathways (Lee *et al.* , 2020).

In inter-plant communication, VOCs modulate receiver plant physiology and directly or indirectly affect other plant holobiome members. VOCs captured by receiver plant wax display fungicidal and bactericidal activity for several days (Camacho-Coronel *et al.* , 2020). GLVs and terpenoid volatiles have strong fungicidal and bactericidal activity*in vitro* and *in planta* (Huang, Sanchez-Moreiras, Abel, Sohrabi, Lee, Gershenzon & Tholl, 2012, Pontin, Bottini, Burba & Piccoli, 2015, Quintana-Rodriguez *et al.* , 2015). VOCs can alter parasitoid attraction and entomopathogenic fungi performance in both donor and receiver plants (Desurmont,

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Xu & Turlings, 2016, Lin *et al.* , 2016, Xu, Desurmont, Degen, Zhou, Laplanche, Henryk & Turlings, 2016). VOC emission in aboveground and below-ground parts may attract or repel herbivores and plant pathogenic nematodes (Ali, Alborn & Stelinski, 2011, D'Alessandro, Erb, Ton, Brandenburg, Karlen, Zopfi & Turlings, 2014, Rasmann, Kollner, Degenhardt, Hiltpold, Toepfer, Kuhlmann, Gershenzon & Turlings, 2005).

Root exudates act as critical triggers to activate resistance in neighboring plants by diffusing through the soil to neighboring roots (Table 1). Root exudates such as SA transfer the SAR signal to neighboring plants and synchronize their microbiomes (Kong, Song, Sim & Ryu, 2020, Orlovskis & Reymond, 2020, Song *et al.* , 2016). Plants exploit microbiome adaptation to facilitate conspecific survival according to kin selection theory, or to compete for heterospecificity. Airborne signals from wound-damaged plants regulated the ALMT1 transporter in receiver Arabidopsis plants to release malic acid into the rhizosphere (Figure 3). Malic acid recruits *B. subtilis* to colonize Arabidopsis roots and induce systemic resistance to different stresses (Rudrappa, Czymmek, Pare & Bais, 2008, Sweeney, Lakshmanan & Bais, 2017). A (−)-loliolide root exudate at a physiological concentration of 5 nmol g^{-1} soil induces the release of the benzoxazinoid compound 2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one (DIMBOA) exudate from wheat roots (Kong *et al.* , 2018). DIMBOA is a putative allelochemical with several other roles in the rhizosphere. DIMBOA regulates the root metabolome and exudation, which have important roles in shaping the root microbiome (Cotton *et al.* , 2019, Kudjordjie, Sapkota, Steffensen, Fomsgaard & Nicolaisen, 2019). DIMBOA-treated plants recruit specific bacterial families and species such as *Pseudomonas putida* , thereby increasing plant resistance to several stresses (Neal & Ton, 2013). *P. fluorescens* increases DIMBOA and primed resistance against the fungal pathogen *Setosphaeria turcica* in maize (Zhou, Ma, Lu, Zhu & Yan, 2020). The populations of bacterial plant pathogens such as Xanthomonadaceae and *Agrobacterium tumefaciens* decreased in benzoxazinoid-treated plants (Cotton *et al.* , 2019, Kudjordjie*et al.* , 2019).

Any change in cumarin, sesquiterpenes, and diadzein by airborne signals and root exudates will change plant microbiomes (Chen, Jiang, Liu, Liu, Zhao, Liu, Gan, Hallab, Wang, He, Ma, Zhang, Jin, Schranz, Wang, Bai & Wang, 2019b, Okutani, Hamamoto, Aoki, Nakayasu, Nihei, Nishimura, Yazaki & Sugiyama, 2020, Stringlis, Proietti, Hickman, Van Verk, Zamioudis & Pieterse, 2018). Activation of defense hormones (e.g., JA and SA) by airborne signals (e.g., MeSA, 3-pentanol, or effectors of aphid/whitefly pest) induces microbiome adaptation in plants (Lee, Lee & Ryu, 2012, Mannaa *et al.* , 2020, Song, Choi & Ryu, 2015, Yang, Yi, Kim, Lee, Lee, Ghim & Ryu, 2011). Microbiome adaptation in these examples reduces disease severity caused by several plant pathogens and pests, probably by recruiting beneficial bacteria such as *B. subtilis* (Lee*et al.* , 2012, Song *et al.* , 2015). The rhizosphere microbiome also modulates root metabolism and exudation by azelaic acid as a potential signal molecule (Figure 3) (Korenblum *et al.* , 2020). Activation of the two JA pathway branches differentially shape the root microbiome. The Arabidopsis mutants *myc2* and*med25* alter root exudate (Figure 3). Similar changes in some categories of root exudate were observed in mutants of both branches, but some root exudates were differentially synthesized. Clostridiales were abundant but declined in mutants of both branches. *Bacillus* ,*Lysinibacillus* , and *Streptomyces* populations increased in the *med25* mutant, whereas the Enterobacteriaceae population increased in the *myc2* mutant (Carvalhais *et al.* , 2015). Med25 has an important role in regulating density recognition in Arabidopsis and changing root architecture by increasing root response to auxin (Munoz-Parra, Pelagio-Flores, Raya-Gonzalez, Salmeron-Barrera, Ruiz-Herrera, Valencia-Cantero & Lopez-Bucio, 2017).

3.4 ? Acoustic and electric signals

Plants utilize acoustic and electric signals as internal and inter-plant signals. A sound vibration signal can be generated by a herbivore walking on the plant, breaking trichomes, chewing the plant, and even by water stress (Caicedo-Lopez, Contreras-Medina, Guevara-Gonzaleza, Perez-Matzumotob & Ruiz-Ruedab, 2020, Kollasch, Abdul-Kaf, Body, Pinto, Appel & Cocroft, 2020). Pest species might be discriminated based on the vibration frequency they produce (Kollasch *et al.* , 2020). Perception of a sound vibration signal modifies plant epigenetics, transcriptome, proteome, and metabolome (Ghosh, Mishra, Choi, Kwon, Won Bae, Park & Bae, 2016, Jung, Kim, Jung, Jeong & Ryu, 2020). Sound vibration signal perception modulates defense hormones such as SA, leading to activation of MAPKs, MYBs, and transcription factors (Body, Neer, C.,

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Lin, Vu & Cocroft, 2019, Ghosh *et al.* , 2016). This upregulation of key enzymes and secondary metabolites, including catalase and PAL, increases the biosynthesis of phenols, alkaloids, terpenes, and oxylipin-derivative VOCs (Body *et al.* , 2019, Ghosh *et al.* , 2016, Kollasch *et al.* , 2020). These metabolites enhance plant resistance or act as signals in plant–plant communication. Jung *et al.* (2020) reported that sound vibration induces resistance against the root pathogen *Ralstonia solanacearum* by modulating cytokinin signaling, increasing aliphatic glucosinolate biosynthesis through epigenetic DNA methylation by H3K27me3, and improving cell wall reinforcement by downregulating miR397b suppression of lignin accumulation–related transcripts. Vibration sensing is an evolutionarily ancient system that arose before vascular plants emerged, as microalga also have mechanosensory proteins that respond to vibration (Paika, Jinb, Simc & N.L., 2018). Electric signals, primarily Ca^{2+} signaling, have important roles in intra- and inter-plant signaling (Choi, Miller, Wallace, Harper, Mittler & Gilroy, 2017, de Toledo, Parise, Simmi, Costa, Senko, Debono & Souza, 2019, Simmi, Dallagnol, Ferreira, Pereira & Souza, 2020). The oomycete pathogen *Pythium aphanidermatum* exploits electric signals to target host roots (Van West, Morris, Reid, Appiah, Osborne, Campbell, Shepherd & Gow, 2002). Both acoustic and electric signals have high transmission speed and good potential for use in precision agriculture (Choi *et al.* , 2017, Kollasch *et al.* , 2020).

3.5 ? Field applications

Although these previous studies have increased our understanding of the signals and mechanisms involved in plant–plant communication, the ultimate goal is to transfer this knowledge to the agricultural field. Field applications can leverage the intrinsic potential of inter-plant signaling by intercropping or rotating crops according to lab results, or by eliciting plant–plant communication with biological and chemical elicitors. Plant defense inducers can be applied to induce volatile emission and trigger plant immunity against insect pests and microbial pathogens (Table 1). MIPVs and HIPVs contain VOCs that inhibit pathogen growth and prime resistance in neighboring plants (Quintana-Rodriguez *et al.* , 2015, Sharifi *et al.* , 2018). Inoculating some plant rows in a field with non-pathogenic strains of plant pathogens, MAMPs, or HAMPs can induce VOCs release and reduce disease severity in all plants in the field. Grapevine inoculation with a sulfated laminarin MAMP increases the emission of terpenes such as (*E,E*)-α-farnesene, β-caryophyllene, and trans-β-ocimene, and subsequently increases resistance to downy mildew disease. VOCs release and disease resistance are significantly positively correlated (Chalal *et al.* , 2015), and the inter-plant signaling activity of these compounds on neighboring plants has been reported elsewhere (Lazazzara, Bueschl, Parich, Pertot, Schuhmacher & Perazzolli, 2018, Quintana-Rodriguez *et al.* , 2015). The flg22 MAMP significantly induces the oxylipin volatiles nonanal, heptanal, and hendecanal (Tu *et al.* , 2017). Nonanal is an inter-plant signal that induces systemic resistance against plant pathogens (Yi *et al.* , 2009).

Inter-plant infochemicals can be applied to volatile emission and trigger immune responses (Ameye, Audenaert, De Zutter, Steppe, Van Meulebroek, Vanhaecke, De Vleesschauwer, Haesaert & Smagghe, 2015). The (*Z*)-3-hexenyl acetate GLV primes JA-dependent signaling against *Fusarium graminearum* in wheat (Ameye *et al.* , 2015). Indole primes the expression of JA-dependent genes and increases JA synthesis against fall armyworm (*Spodoptera frugiperda*) in rice (Ye *et al.* , 2019). Some infochemicals may induce disease susceptibility depending on the pathosystem. GLVs induce maize susceptibility against *Colletotrichum graminicola* by suppressing SA-dependent pathways (Gorman, Christensen, Yan, He, Borrego & Kolomiets, 2020). Plant growth–promoting and endophytic bacteria can induce plant volatiles synthesis to attract parasitoids and entomopathogens (Bell, Naranjo-Guevara, Santos, Meadow & Bento, 2020, Disi, Mohammad, Lawrence, Kloepper & Fadamiro, 2019, Maggini, Bandeira Reidel, De Leo, Mengoni, Rosaria Gallo, Miceli, Biffi, Fani, Firenzuoli, Bogani & Pistelli, 2020). By contrast, there is an example that endophytic microbes do not have a significant effect on plant VOCs profiles and the behavior of herbivores and their parasitoids (Moisan, Lucas-Barbosa, Villela, Greenberg, Cordovez, Raaijmakers & Dicke).

Plant–plant communication can be enhanced by introducing fungal networks into the soil between plants and by triggering fungal spore germination and root colonization with strigolactones and beneficial bacteria. Mycorrhiza and endophytic fungi such as *Piriformospora indica* can transfer infochemical signals between plant species (Song *et al.* , 2014, Vahabi *et al.* , 2018). Soil inoculation with these fungi or promoting their

populations by conservative and organic agriculture can improve inter-plant signaling and plant priming for imminent challenges. Soil disturbance in intense tillage systems negatively affects mycorrhizae communities (Wang, Li, Li, Zhao & Liao, 2020b). Mycorrhiza colonization is controlled by strigolactones and phosphorus availability (Lopez-Raez *et al.* , 2017, Waters *et al.* , 2017). Thus, reduced application of phosphorus fertilizers and increased application of phosphate-solubilizing bacteria and mycorrhiza can improve plant colonization by mycorrhiza. Beneficial microbes also can promote root colonization by mycorrhiza even in non-mycorrhiza plants (Poveda, Hermosa, Monte & Nicolás, 2019).

Plant–plant communication can be maximized by managed intercropping to locate aboveground and below-ground plant parts in close proximity to chemicals released by neighbor plants, which can directly inhibit the germination and growth of pathogenic fungi and bacteria or repel herbivores from fields (Lazazzara *et al.* , 2018, Quintana-Rodriguez *et al.* , 2015, Yang, Zhang, Qi, Mei, Liao, Ding, Deng, Fan, He, Vivanco, Li, Zhu & Zhu, 2014, Zhou, Cen, Tian, Wang & Zhang, 2019). Volatiles from resistant cultivars contain volatiles that can directly inhibit pathogen growth or induce systemic resistance in neighbor susceptible cultivars (Lazazzara *et al.* , 2018, Quintana-Rodriguez *et al.* , 2015). In some cases, a "bait" species can be planted in field borders to attract herbivores away from the main crop via HIPV release. Inter-plant signals can suppress plant pathogens directly or indirectly through microbiome adaptation. Intercropping of aerobic rice and watermelon reduces disease severity of *Fusarium oxysporum* in watermelon (Ren, Su, Yang, Xu, Huang & Shen, 2008). Rice root exudates reduce pathogen spore germination up to 41% and alter the root microbiome community structure in favor of *Actinomycetes* . Similarly, corn can act as a biological wall between pepper rows to inhibit *Phytophthora capsici* growth and promote the root microbiome (Yang *et al.* , 2014). DIMBOA is a density-dependent allelochemical that suppresses plant pathogens in densely cropped maize rows. Intercropped plants can emit infochemicals that alter the transcriptomes of neighboring plants to cope with pathogens. RNA-seq results suggest that tall fescue root exudate containing putrescine and cyclohexane-1,2-diol stimulates the expression of genes related to defense hormones and pathogenesis-related proteins in tomato, and reduces stem rot disease (Zhou *et al.* , 2019).

Plant debris functions as a modulator and infochemical for the next plant generation and rhizosphere micro-biome. Infochemicals can remain in the ecosystem after plant death or harvest and act as signals for the next crop generation. Infochemicals have different chemical stabilities under different conditions. Plant debris in minimum-tillage and no-tillage systems may enhance slow-release of infochemicals. Plant debris can affect the next crop by modifying the soil microbiome community and activity, by increasing soil fertility, or by acting as an infochemical source (Veen, Fry, ten Hooven, Kardol, Morriën & De Long, 2019, Wang, Wu, Wang, Alabady, Parson, Molumo & Fankhauser, 2020a). Plant debris from root and aerial parts contains information about plant identity, life history, and memory of biotic/abiotic stresses. *Medicago truncatula* growth and endophytic fungi are affected by neighboring plants and by plants from the previous season. Thus, both intercropping and crop rotation affect the ecological performance of alfalfa as the holobiome (Vannier *et al.* , 2020). Rotation in hydroponic systems also affects the next crop's performance. *Vicia faba* plants infested by *Acyrthosiphon pisum* release soluble chemicals that increase the attractiveness of the next plant parasitoid *Aphidius ervi* . Similarly, lima bean infested by *Tetranychus urticae* increase the next season plant's attraction of the predatory mite *Phytoseiulus persimilis* (Delory *et al.* , 2016, Guerrieri, Dong & Bouwmeester, 2019).

Large-scale formulation and application of inter-plant infochemicals is a promising approach in integrated crop management. These compounds can be considered as synthetic pesticide alternatives and can reduce their application dose by combining synthetic pesticides and pest lure volatiles to attract and kill pest (Martel, Alford & Dickens, 2007). However, infochemicals are highly reactive compounds with short half-lives under natural conditions. Plant should be treated with these compounds at the proper time under optimum conditions to avoid neutral or negative effects on plant growth and defense. Micro- and nano-encapsulation of infochemicals in natural and synthetic polymers for slow- or controlled-release improves their effects on plant health and volatile emission (Oliveira, Varanda & Félix, 2016, Wang, Liu, Zhan & Liu, 2019). Plant virus particles can be used to deliver infochemicals into the rhizosphere (Chariou, Dogan, Welsh, Saidel, Baskaran & Steinmetz, 2019). The formulation technologies and field applications of infochemicals is

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reviewed elsewhere (Sharifi & Ryu, 2018a, Sharifi & Ryu, 2020).

4 ? CONCLUDING REMARKS

The holobiont is an evolutionary collaboration that assembles individual species with unique contributions that benefit all members and enhance holobiont performance and survival. Plant members of the holobiome compete with kin and non-kin plants for light, water, and nutrients (Ballare & Austin, 2019, Effah, Holopainen & McCormick, 2019, Hodge, Fitter & Robinson, 2013, Hortal *et al.*, 2017). However, only some of the competition mechanisms rely on the plant genome. Plant microbiota have pivotal roles in nutrient solubility and uptake, especially nitrogen, phosphorus, and iron (Adesemoye, Torbert & Kloepper, 2008, Sharifi, Ahmadzadeh, Sharifi-Tehrani & Talebi-Jahromi, 2010). Microbiota also improve water use efficiency and osmotic stress response (Fan, Hu, Huang, Huang, Li & Palta, 2015, Sharifi & Ryu, 2018c). The plant holobiome leverages the collection of its member genes to optimize performance and survival. Plant health also depends on the hologenome. Plants have spatiotemporal layers of defense consisting of rhizosphere microbes, endophytes, PTI, ETI, and recruited natural enemies; each of these can efficiently suppress specific groups of attackers (Carrion *et al.*, 2019, Sharifi & Ryu, 2017). Because of these advantages conferred by microbiota, plants donate 10–30% of their carbon and nitrogen to the rhizosphere to organize their microbiota. Mycorrhizae are long-term plant partners that can expand the rhizosphere into an area called the mycorrhizosphere. Microbes also manage their rhizosphere conditions by modulating mycorrhizae growth and inducing root metabolism and exudation (Korenblum *et al.*, 2020).

In competitive environments, plant species dominance partly depends on the microbiome. The microbiome of dominant plants is more stable during competition, and the soil microbiome resulting from plant competition is shaped by the dominant plant species (Hortal *et al.*, 2017). Dominant plants may have an intrinsic ability to collaborate with beneficial microbiota to enhance competitiveness. For example,*Lycium intricatum* exploits *Halomonas* and*Salinimicrobium* genera in water-competitive environments (Hortal*et al.*, 2017).

Domestication, plant breeding, and agricultural practices change the intrinsic ability of plants to establish diverse highly functional microbiota (Hassani, Duran & Hacquard, 2018, Martinez-Romero, Noyola, Taype, Martinez-Romero & Davila, 2020, Wang *et al.*, 2020b). Key metabolites or sensory proteins may be lost during domestication, resulting in the loss of groups of microbiota or of the ability to recruit natural enemies (Kollner, Held, Lenk, Hiltpold, Turlings, Gershenzon & Degenhardt, 2008, Martinez-Romero *et al.*, 2020). Therefore, plant breeders and genetic engineers should have a holistic view of plants as members of the holobiome. Otherwise, small changes in key ecology-related genes may substantially affect plant performance, a phenomenon called the butterfly effect.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

Table 1. Effect of plant–plant communication via volatile organic compounds and root exudates on the suppression of plant pathogens.

Donor plant	Receiver plant	Signal molecule	Target pathogen	Reference
Volatile organic compounds	**Volatile organic compounds**			

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Donor plant	Receiver plant	Signal molecule	Target pathogen	Reference
Lima bean	Lima bean	VOC, nonanal	*Pseudomonas syringae* pv. syringae PR-2	(Yi *et al.*, 2009)
Tomato	Tomato	(*Z*)-3-hexenyl propionate (*Z*)-3-hexenyl butyrate	*Pseudomonas syringae* pv. tomato stomatal closure	(Lopez-Gresa, Paya, Ozaez, Rodrigo, Conejero, Klee, Belles & Lison, 2018)
Maize	Maize	(*Z*)-3-hexen-1-yl acetate, (*Z*)-3-hexenal, linalool and β-caryophyllene	*Fusarium* spp.	(Piesik, Lemnczyk, Skoczek, Lamparski, Bocianowski, Kotwica & Delaney, 2011)
Barley and wheat	Barley and wheat	GLV, (*Z*)-b-ocimene and linalool	*Fusarium* spp.	(Piesik *et al.*, 2013)
Wheat	Wheat	GLVs, fatty acid derivatives, benzenoids, and terpenoid	*Puccinia triticina*	(Castelyn *et al.*, 2014)
Lima bean	Lima bean	Limonene, linalool, nonanal, methyl salicylate, and methyl jasmonate	*Colletortichum lindemuthianum*	(Quintana-Rodriguez *et al.*, 2015)
Tobacco	Tobacco	Methyl salicylate	Tobacco mosaic virus (TMV)	(Shulaev, Silverman & Raskin, 1997)
Tea (*Camellia sinensis*)	Tea	(*E*)-nerolidol	*Colletotrichum fructicola*	(Chen, Zhang, Cai, Li, Bian, Luo, Li, Chen & Xin, 2020)
Arabidopsis thaliana	*A. thaliana*	α- and β-pinene	*P. syringae* pv. *tomato*	(Riedlmeier, Ghirardo, Wenig, Knappe, Koch, Georgii, Dey, Parker, Schnitzler & Vlot, 2017)
Maize	Maize	GLVs , terpenes Shikimic acid pathway derivatives	*Pantoea ananatis*	(Delaney, Breza-Boruta, Lemańczyk, Bocianowski, Wrzesińska, Kalka & Piesik, 2015)

Root exudates

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Donor plant	Receiver plant	Signal molecule	Target pathogen	Reference
Poncirus trifoliata	*P. trifoliata*	Salicylic acid (SA)	*Xanthomonas axonopodis* pv. *citri*	(Zhang, Zou, Liu & Wu, 2019)
Maize	Pepper	2,4-Dihydroxy-7-methoxy-2H-1,4-benzoxazin-3(4H)-one, 6-methoxy-2-benzoxazolinone, benzothiazole, and 2-(methylthio)-benzothiazole	*Phytophthora capsici*	(Yang *et al.*, 2014)
Tobacco	Tobacco	SA	*Ralstonia solanacearum* and *P. syringae* pv. tabaci	(Cheol Song, Sim, Kim & Ryu, 2016)
Arabidopsis thaliana	*A. thaliana*	Root-derived signal(s)	*Pseudomonas syringae pv.* tomato	(Orlovskis & Reymond, 2020)

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Figure Legends

Figure 1. Wired and wireless phytobiome communication. Clonal plants (right) communicate via physical connections (e.g., stolons and rhizomes) or VOCs. Plants also communicate via dodder and mycorrhiza (left). Reciver plants can act as nodes to transfer defense signals against pests and pathogens to neighboring conspecific and heterospecific plants. Volatiles and root exudates recived by neighboring plants modulate receiver plant defense systems, attract parasitoids and entemopathogens, and induce plant microbiome remodeling to protect plants against imminent stress conditions.

Figure 2. Illustration of the signal input-transfer-output model in plant –plant communication. Molecular patterns, volatiles, and effector proteins of pests and pathogens elicit plant signaling pathways that promote volatiles emission and root exudation. Plant signals can be delivered to neighboring plants through the atmosphere or soil (wireless communication), or transferred through mycorrhiza, fungi, and odder (wired communication). Signals can be converted to their active form by receiver plant proteins. Signal perception by neighbor plants activates signaling pathways and phosphorylation cascades, which subsequently induce the expression of defense-related proteins and metabolites. Signal perception also changes the root exudate and recruits beneficial microbes. MAMPs, microbe-associated molecular patterns; HAMPs, herbivore-associated molecular patterns; VOCs, volatile organic compounds; GLVs, green leaf volatiles; BZ, benzoxazinoid; SA, salicylic acid; MeSA, methyl salicylate; JA, jasmonic acid; MEP, methylerythritol phosphate; MVA, mevalonic acid; MAPKs, mitogen-activated protein kinases; TFs, transcription factors.

Figure 3. Signals from neighboring plants modulate signaling pathways in receiver plants and induce microbiome remodeling. Signals can be sensed by reciver proteins (e.g., ETR1 sensor for ethylene) or coverted to active signals [e.g., SABP2 for salicylic acid (SA)]. Signals are transmitted through well-characterized downstream pathways that may cross-talk with each other. These signaling pathways regulate defense mechanisms against different groups of attackers and induce plant microbiome remodeling by changing root exudation, thereby adapting the plant holobiome to respond to imminent threats. MeSA, methyl salicylate; $SABP_2$, SA-BINDING PROTEINS 2; NPR, NON-EXPRESSER OF PR genes; G3P, glycerol-3-phosphate; ETR1, ETHYLENE RESPONSE 1; EIN2, ETHYLENE INSENSITIVE 2; CTR1, CONSTITUTIVE TRIPLE RESPONSE 1; ORA59, OCTADECANOID-RESPONSIVE ARABIDOPSIS 59; MeJA, methyl jasmonate; Med25, Mediator 25; JAZ, JASMONATE ZIM DOMAIN protein; SCF^{COI1}, Skp1-Cul1-F-box protein CORONATINE INSENSITIVE 1; FIT1, FE-DEFICIENCY-INDUCING TRANSCRIPTION FACTOR1; FRO2, FERRIC REDUCTASE OXIDASE 2; IRT1, IRON-REGULATED TRANSPORTER 1; IAA, indole-3-acetic acid; AUX1/LAX, AUXIN RESISTANT 1/LIKE AUX1; ALMT1, ALUMINUM-ACTIVATED MALATE TRANSPORTER; CDPK, Ca^{2+}-dependent proteinkinases; CIPK, calcineurin B like proteins (CBL)-interacting protein kinase.