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Social networking in crop plants: Wired and wireless cross-plant communications

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Abstract

The plant-associated microbial community (microbiome) has an important role in plant–plant communications. Plants decipher their complex habitat situations by sensing the environmental stimuli and molecular patterns and associated with microbes, herbivores and dangers. Perception of these cues generates inter/intracellular signals that induce modifications of plant metabolism and physiology. Signals can also be transferred between plants via different mechanisms, which we classify as wired- and wireless communications. Wired communications involve direct signal transfers between plants mediated by mycorrhizal hyphae and parasitic plant stems. Wireless communications involve plant volatile emissions and root exudates elicited by microbes/insects, which enable inter-plant signalling without physical contact. These producer-plant signals induce microbiome adaptation in receiver plants via facilitative or competitive mechanisms. Receiver plants eavesdrop to anticipate responses to improve fitness against stresses. An emerging body of information in plant–plant communication can be leveraged to improve integrated crop management under field conditions.

KEYWORDS
dodder, herbivore-induced plant volatiles, holobiont, microbe-induced plant volatiles, microbiome adaptation, mycorrhiza

1 | INTRODUCTION

Plants adapt to stress via sensor elicitation, signalling 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 defence 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 et al., 2018; Yi, Heil, Adame-Alvarez, Ballhorn, & Ryu, 2009). The plant can exploit the unique capabilities of its symbionts including the mycorrhizal network, dodder (*Cuscuta* spp.) and endophytic fungi, which directly prime plant defence responses or transfer inter-plant signals (da Trindade et al., 2019; Hettenhausen et al., 2017; Vahabi et al., 2018). The plant microbiome and macrobiome 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 plant–plant communications that improve plant defence against pathogenic microbes. From multiple layers of plant–
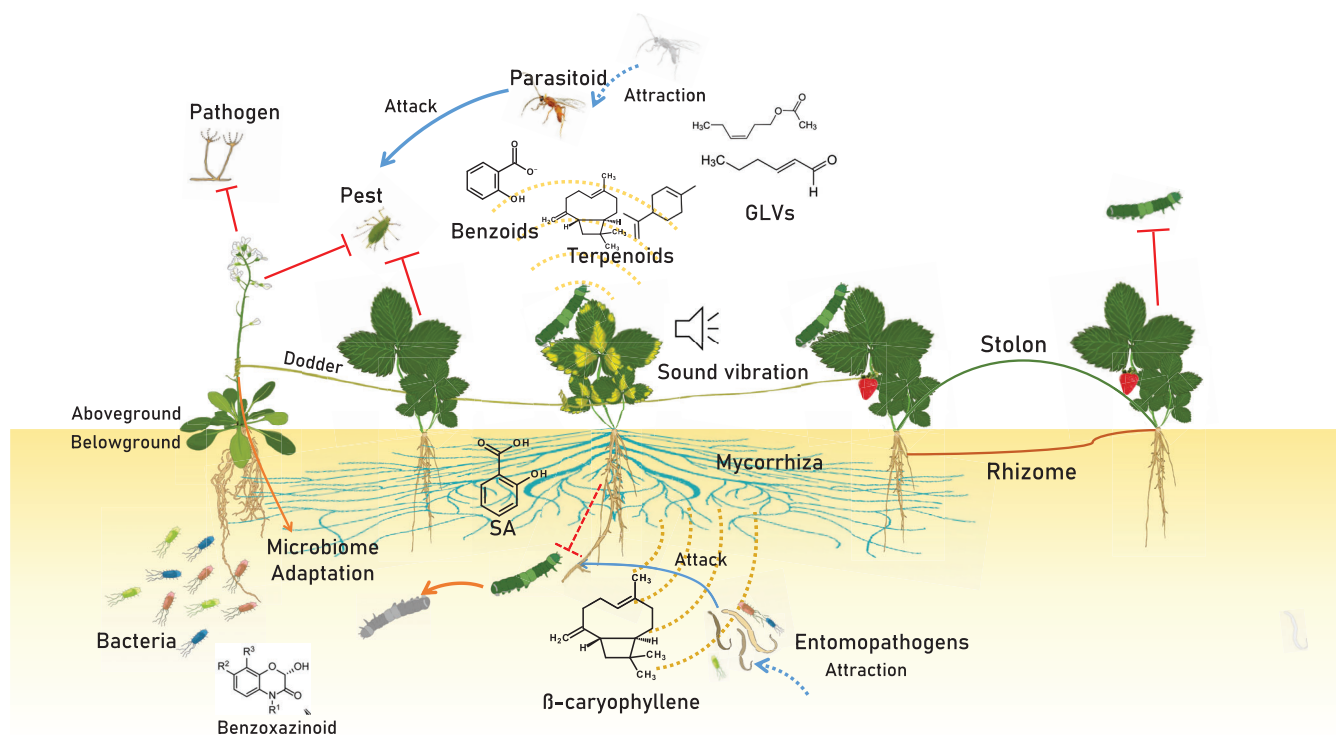
FIGURE 1   Wired and wireless phytobiome communication. Clonal plants (right) communicate via physical connections (e.g. stolons and rhizomes) or VOCs. Plants also communicate via dodder and mycorrhiza (left). Receiver plants can act as nodes to transfer defence signals against pests and pathogens to neighbouring conspecific and heterospecific plants. Volatiles and root exudates received by neighbouring plants modulate receiver plant defence systems, attract parasitoids and entemopathogens and induce plant microbiome remodelling to protect plants against imminent stress conditions [Colour figure can be viewed at wileyonlinelibrary.com]

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 defence 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 et al., 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 et al., 2014; Qian, Li, Han, & Sun, 2010; Semchenko, John, & Hutchings, 2007).

Physical connections via stolon and rhizome can mitigate abiotic stress by facilitating the transfer/exchange of nutrients and metabolites, or by modulating resource use efficiency (Figure 1; Roiloa, Antelo, & Retuerto, 2014). Defence signals can be transferred via phloem from older to younger ramets to induce systemic resistance in young ramets. Older ramets do not receive defence signals from younger clones due to the direction of source-sink gradient flow (Gómez & Stuefer, 2006). In *Trifolium repens*, a defence signal against *Mamestra brassicae* larvae can be transferred to younger ramets within 35–51 hr depending on genotypic variation. Induced but undamaged ramets lose their resistance after 28 days (Gómez, Van Dijk, & Stuefer, 2010). Besides direct plant–plant links via plant parts, higher parasitic plants are also an important link in wired communications that enhance plant fitness.

2.2 | Wired connections between independent plants via dodder-mediated interspecific signalling

Dodders (*Cuscuta* spp.) are plant holoparasites that acquire water and nutrients from host plants via the haustorium, which physically

> **BOX 1   Definitions: holobiont, holobiome, microbiome**
>
> 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 the survival of the holobiont.
>
> The holobiome includes all living organisms, their genetic materials and their primary and secondary metabolites, as well as the molecules produced within a particular habitat (Berg et al., 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 et al., 2018; Gu et al., 2016).

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 et al., 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 neighbouring plant signals transferred through the common dodder network. Although there are few reports on the role of the common dodder network in inter-plant signalling, the results indicate that these transferred signals are important in biotic/abiotic stress responses. When a host of the dodder plant is under abiotic stress such as 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 neighbouring 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, et al., 2020).

Plants infected with different herbivorous insects transfer relatively long-distance signals to conspecific and heterospecific neighbours 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 (*Cuscuta australis*) by up to 58 and 41%, respectively. Aphids can modulate hormonal signalling 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 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 (Tedersoo, Bahram, & Zobel, 2020). 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 neighbouring 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 m 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 (Bennett, Cahill, & van der Heijden, 2016; Hortal et al., 2017).

Plants exploit mycorrhizae fungi for long-distance transfer of plant signals and allelochemicals. *Tagetes tenuifolia* secretes the

lipophilic allelopathic compound thiophene and the hydrophilic allelo-pathic compound imazamox, which can diffuse more than 12 cm via the common mycorrhiza network (Barto et al., 2011). Mycorrhizae fungi can translocate defence signals to neighbouring unstressed plants, similar to dodder. Tomato plants infected with the nectrotrophic pathogenic fungus *Alternaria solani* transfer a signal to non-infected neighbours at 18 hr post-inoculation via mycorrhizae hypha. In the receiver plants, the relative expression levels of defence-related genes such as phenylalanine ammonia-lyase (PAL), lipoxygenase, polyphenol oxidase and pathogenesis-related proteins (PR1, PR2 and PR4) were the same as those in the donor plants (Song et al., 2010). Alaux, Naveau, Declerck, and Cranenbrouck (2020) also set up a sophisticated in vitro experiment to confirm the role of mycorrhizae in plant–plant signal transduction. The results showed that a *Phytophthora infestans* infected tomato plant could transfer a signal to healthy neighbours via mycorrhizae hypha to activate the transient expression of JA related genes. Signal transduction via the common mycorrhiza network also has been detected for herbivore-damaged plants (Babikova et al., 2013; Song et al., 2014).

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 neighbouring *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 neighbouring (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 neighbouring host (Andika et al., 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 et al., 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 induced by microbes, insects and environmental stimuli. Infochemicals diffuse via air and soil pores to reach neighbour plants.

Receiver plants can amplify the released infochemical signals to expand the effective infochemical signalling zone. Infochemicals perceived by the receiver plants can act as kin recognition signals, growth inhibitors (allelopathy), growth stimulators and defence signals (Karban, Shiojiri, Ishizaki, Wetzel, & Evans, 2013; Kong et al., 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 neighbouring plants through a facilitative or competitive mechanism (Carvalhais et al., 2015; Li, Zhao, & Kong, 2020; 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. 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 neighbour organisms to determine the presence and identity of neighbouring plants. Receiver plants recognize the degree of phylogenetical relationship of neighbour plants to discriminate kin and non-kin plants (Biedrzycki, Jilany, Dudley, & Bais, 2010; Yang, Li, Xu, & Kong, 2018). In most cases, signals from healthy plants can affect neighbouring plants by modifying biomass allocation, lateral root formation and chlorophyll and phenolic compound biosynthesis, or directly inhibiting seed germination (Delory, Delaplace, Fauconnier, & du Jardin, 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). Exposing potato plants to healthy onions changes the profile of potato volatiles such that they repel aphids and attract ladybird beetles, which are aphid predators (Ninkovic et al., 2013; Vucetic et al., 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).

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 et al., 2010). Isoprene alleviates plant oxidative stress (van Doorn et al., 2020).

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. 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 et al., 2015; Sharifi et al., 2018).

VOC profiles are conventionally defined based on what triggers their emission. They include herbivore-induced plant volatiles (HIPVs), oviposition-induced plant volatiles, microbe-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. Green

leaf volatiles (GLVs) are categorized as HIPVs, especially for chewing insects, but GLVs also are emitted from microbial pathogen-infected plants (Ameye et al., 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 et al., 2020).

Plants emit VOCs in response to signalling 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 et al., 2017; Sharifi et al., 2018; Wu et al., 2017). These elicitors activate defence-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 et al., 1997; Alborn et al., 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*
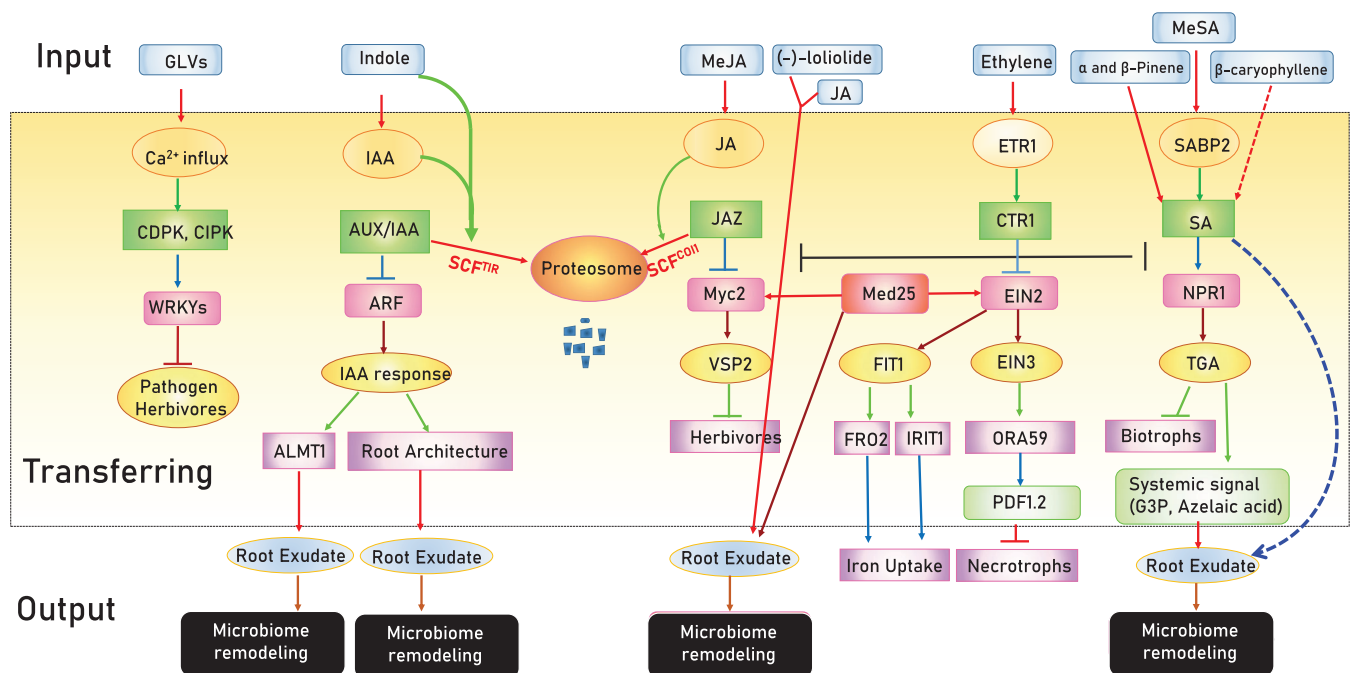

FIGURE 2 Signals from neighbouring plants modulate signalling pathways in receiver plants and induce microbiome remodelling. Signals can be sensed by receiver proteins (e.g. ETR1 sensor for ethylene) or converted to active signals [e.g. SABP2 for salicylic acid (SA)]. Signals are transmitted through well-characterized downstream pathways that may cross-talk with each other. These signalling pathways regulate defence mechanisms against different groups of attackers and induce plant microbiome remodelling by changing root exudation, thereby adapting the plant holobiome to respond to imminent threats. ALMT1, aluminium-activated malate transporter; AUX1/LAX, auxin resistant 1/LIKE AUX1; CDPK, Ca^{2+}-dependent protein kinases; CIPK, calcineurin B like proteins (CBL)-interacting protein kinase; CTR1, constitutive triple response 1; EIN2, ethylene insensitive 2; ETR1, ethylene response 1; FIT1, FE-deficiency-inducing transcription factor 1; FRO2, ferric reductase oxidase 2; G3P, glycerol-3-phosphate; IAA, indole-3-acetic acid; IRT1, iron-regulated transporter 1; JAZ, Jasmonate Zim domain protein; Med25, mediator 25; MeJA, methyl jasmonate; MeSA, methyl salicylate; NPR, non-expresser of PR genes; ORA59, octadecanoid-responsive Arabidopsis 59; SABP2, SA-binding proteins 2; SCFCOI1, Skp1-Cul1-F-box protein coronatine insensitive 1 [Colour figure can be viewed at wileyonlinelibrary.com]

frugiperda) suppress HIPVs in maize, but not in cotton (De Lange et al., 2020).

In some plant pathogens, PAMPs (e.g. flg22, laminarin and glucan) and effector proteins (e.g. 2b) can modify plant VOCs (Chalal et al., 2015; Leitner et al., 2008; Sobhy, Bruce, & Turlings, 2018; Tu et al., 2017; Tungadi et al., 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).

Signalling pathways (e.g. SA- and JA-dependent pathways) leading to systemic resistance in inoculated and neighbouring plants have important roles in volatile biosynthesis (Orlovskis & Reymond, 2020; Wenig et al., 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 et al., 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 et al., 2013) can modulate VOC emissions and attract pests and their parasitoids.

3.1.3 | Root exudates as inter-plant signals

Plants release large amounts of root exudates into the soil, where they act as carbon and nitrogen sources or cues for rhizosphere organisms. The profile of root exudates can be affected by biotic and abiotic stimuli. Soil dwelling organisms and roots of neighbouring plants use some of these root exudates as a source of information
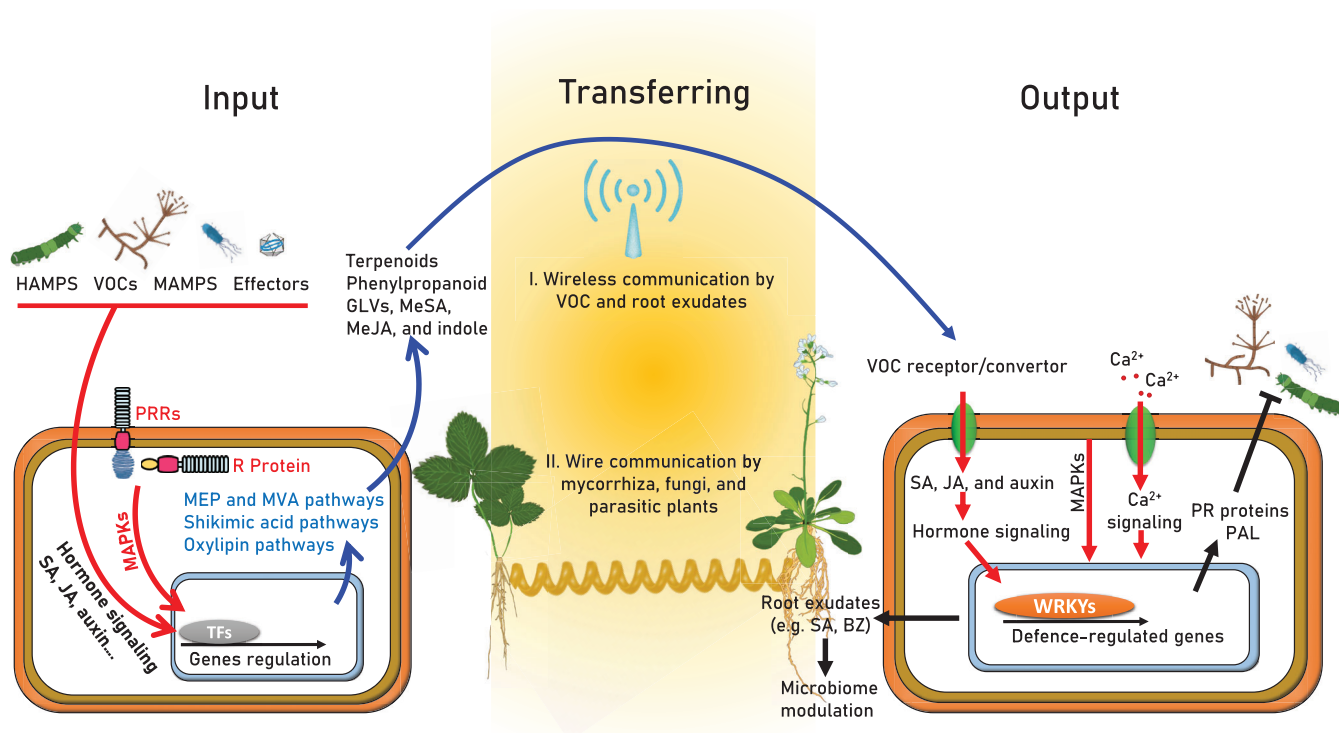

FIGURE 3 Illustration of the signal input-transfer-output model in plant–plant communication. Molecular patterns, volatiles and effector proteins of pests and pathogens elicit plant signalling pathways that promote volatiles emission and root exudation. Plant signals can be delivered to neighbouring 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 neighbour plants activates signalling pathways and phosphorylation cascades, which subsequently induce the expression of defence-related proteins and metabolites. Signal perception also changes the root exudate and recruits beneficial microbes. BZ, benzoxazinoid; GLVs, green leaf volatiles; HAMPs, herbivore-associated molecular patterns; JA, jasmonic acid; MAMPs, microbe-associated molecular patterns; MAPKs, mitogen-activated protein kinases; MEP, methylerythritol phosphate; MeSA, methyl salicylate; MVA, mevalonic acid; SA, salicylic acid; TFs, transcription factors; VOCs, volatile organic compounds [Colour figure can be viewed at wileyonlinelibrary.com]

(Bais, 2006; Biedrzycki et al., 2010; Carvalhais et al., 2015; Khashi u Rahman, Zhou, & Wu, 2019; Sharifi & Ryu, 2017). Plants employ root exudates to discriminate between kin and non-kin neighbour plants. Rice use allantoin as a cue to recognize kin cultivars and respond to it by shifting root biomass allocation and increasing grain yield (Yang et al., 2018). An allantoin mutant of Arabidopsis was reported to be susceptible to *P. syringae* and *Pectobacterium carotovorum*. Exogenous application of allantoin also induces JA-responsive genes, such as MYC2 (Table 1; Takagi et al., 2016). Root exudates such as (−)-loliolide, jasmonic acid and salicylic acid act as inter-plant signals and plant defence inducers (Cheol Song et al., 2016; Kong et al., 2018; Li, Zhao, & Kong, 2020). (−)-loliolide from

barnyardgrass (*Echinochloa crus-galli*) root exudates induces the biosynthesis of the rice allelochemicals, momilactone B and tricin (Li, Zhao, & Kong, 2020), which can reduce the disease severity of several rice pathogens, such as *Piricularia oryzae*, *R. solani* and *Fusarium oxysporum* (Table 1; Kong et al., 2010; Zhao et al., 2018).

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 centimetres to several

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	References
Volatile organic compounds				
Lima bean	Lima bean	Volatile organic compound, nonanal	*P. syringae* pv. syringae PR-2	Yi et al. (2009)
Tomato	Tomato	(Z)-3-hexenyl propionate (Z)-3-hexenyl butyrate	*P. syringae* pv. tomato stomatal closure	Lopez-Gresa et al. (2018)
Maize	Maize	(Z)-3-hexen-1-yl acetate, (Z)-3-hexenal, linalool and β-caryophyllene	*Fusarium* spp.	Piesik et al. (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	Shulaev, Silverman, and Raskin (1997)
Tea (*Camellia sinensis*)	Tea	(E)-nerolidol	*Colletotrichum fructicola*	Chen et al. (2020)
A. thaliana	*A. thaliana*	α- and β-pinene	*P. syringae* pv. tomato	Riedlmeier et al. (2017)
Maize	Maize	GLVs, terpenes Shikimic acid pathway derivatives	*Pantoea ananatis*	Delaney et al. (2015)
Root exudates				
Poncirus trifoliata	*P. trifoliata*	Salicylic acid	*Xanthomonas axonopodis* pv. *citri*	Zhang, Zou, Liu, and 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	*P. capsici*	Yang et al. (2014)
Tobacco	Tobacco	Salicylic acid	*R. solanacearum* and *P. syringae* pv. tabaci	Cheol Song, Sim, Kim, and Ryu (2016)
A. thaliana	*A. thaliana*	Root-derived signal(s)	*P. syringae* pv. tomato	Orlovskis and Reymond (2020)
E. crus-galli	Rice[a]	(−)-loliolide	*P. oryzae* *F. oxysporum* *R. solani*	Kong, Xu, Zhang, and Zhang (2010), Li, Zhao, and Kong (2020) and Zhao, Cheng, Guo, Duan, and Che (2018)
Rice	Rice[a]	Allantoin	*P. syringae* *P. carotovorum*	Takagi et al. (2016) and Yang et al. (2018)

[a]This information was obtained from several reports, some of which reported these chemicals as inter-plant signals and others as their effects on plant pathogens.

metres according to their chemical structure and vectors such as mycorrhiza and dodder. Wheat infected by *Fusarium culmorum* transfers signals to neighbour plants located 1–3 m 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 signalling (Chen, Yang, et al., 2019; Piesik et al., 2013; Wenig et al., 2019). Thus, neighbouring plants amplify signals in clusters of receiver plants. However, the regulation of induced signalling 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 et al. (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 hr, whereas more distant plants responded after 1 hr. In this study, focal plant stomata remained closed for 24 hr, 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* neighbours to improve their acclimation (Falik et al., 2012).

Wenig et al. (2019) showed that monoterpenes such as 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 defence signal can self-stimulate in receiver plants and activate SA hormones (Chen, Yang, et al., 2019).

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

The transferred signal is perceived by neighbouring (receiver) plants and augments biotic/abiotic stress resistance responses. 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 lead to the discovery of additional receptors for plant VOCs.

Recent studies identified different mechanisms whereby receiver plants perceive VOCs from neighbour 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 et al., 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 (Figures 2 and 3; Bailly et al., 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 et al., 2014). Some GLVs induce plasma membrane potential depolarization in receiver plants, thereby activating reactive oxygen species (ROS) and calcium signalling (Figure 2; Zebelo, Matsui, Ozawa, & Maffei, 2012).

The perception of VOCs modifies the transcriptome, proteome and metabolome in receiver plants (Kwon et al., 2010; van Dam & Bouwmeester, 2016; Zhang et al., 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 defence-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 defence pathways and VOC emission profiles in healthy neighbours. By contrast, primed receiver plants mount a specific set of defence mechanisms based on the type of attacker (Moreira et al., 2018).

Infochemicals from neighbour 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 (Figures 2 and 3; Dombrowski et al., 2019; Dombrowski & Martin, 2018; Lee, Kim, Lee, Ahn, & Ryu, 2020; Mirabella et al., 2015; Wenig et al., 2019; Ye, Glauser, Lou, Erb, & Hu, 2019). D-Lactic acid secreted by the microalga *Chlorella fusca* primed defence in *Arabidopsis thaliana* against *P. 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 et al., 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, Xu, & Turlings, 2016; Lin et al., 2016; Xu et al., 2017). VOC emission in aboveground and below-ground parts may attract or repel herbivores and plant pathogenic nematodes (Ali, Alborn, & Stelinski, 2011; D'Alessandro et al., 2014; Rasmann et al., 2005).

Root exudates act as critical triggers to activate resistance in neighbouring plants by diffusing through the soil to neighbouring roots. Root exudates such as SA transfer the SAR signal to neighbouring 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 et al., 2019; Okutani et al., 2020; Stringlis et al., 2018). Activation of defence 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 et al., 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 et al., 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 et al., 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 et al., 2016; Jung, Kim, Jung, Jeong, & Ryu, 2020). Sound vibration signal perception modulates defence hormones such as SA, leading to activation of MAPKs, MYBs and transcription factors (Body et al., 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 signalling, 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, Jin, Sim, & Jeon, 2018).

Electric signals, primarily Ca^{2+} signalling, have important roles in intra- and inter-plant signalling (Choi et al., 2017; de Toledo et al., 2019; Simmi, Dallagnol, Ferreira, Pereira, & Souza, 2020). The oomycete pathogen *Pythium aphanidermatum* exploits electric signals to target host roots (Van West et al., 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 signalling by intercropping or rotating crops according to lab results, or by eliciting plant–plant communication with biological and chemical elicitors.

Plant defence inducers can be applied to induce volatile emission and trigger plant immunity against insect pests and microbial pathogens. MIPVs and HIPVs contain VOCs that inhibit pathogen growth and prime resistance in neighbouring plants (Quintana-Rodriguez et al., 2015; Sharifi et al., 2018). Inoculating some plant rows in a field with non-pathogenic strains of plant pathogens, microbe-associated molecular patterns (MAMPs), or herbivore-associated molecular patterns (HAMPs) can induce VOC 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 signalling activity of these compounds on neighbouring plants has been reported elsewhere (Lazazzara et al., 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 alter volatile emission profiles and trigger immune responses (Ameye et al., 2015). (Z)-3-hexenyl acetate GLV primes JA-dependent signalling against *Fusarium graminearum* in wheat (Ameye et al., 2015). Indole primes the expression of JA-dependent genes and increases JA synthesis against fall armyworm (*S. frugiperda*) in rice (Ye et al., 2019). Some infochemicals may induce disease susceptibility depending on the pathosystem. Green leaf volatiles (GLVs) induce maize susceptibility against *Colletotrichum graminicola* by suppressing SA-dependent pathways (Gorman et al., 2020). Plant growth–promoting and endophytic bacteria can induce plant volatile synthesis to attract parasitoids and entomopathogens (Bell, Naranjo-Guevara, Santos, Meadow, & Bento, 2020; Disi, Mohammad, Lawrence, Kloepper, & Fadamiro, 2019; Maggini et al., 2020). By contrast, there has been one report showing that endophytic microbes do not have a significant effect on plant VOC profiles and the behaviour of herbivores and their parasitoids (Moisan et al., 2020).

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 *P. 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 signalling and plant priming for imminent challenges. Soil disturbance in intense tillage systems negatively affects mycorrhizae communities (Wang, Li, Li, Zhao, & Liao, 2020). Mycorrhiza colonization is controlled by strigolactones and phosphorus availability (Lopez-Raez, Shirasu, & Foo, 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 can also 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 neighbour 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 et al., 2014; Zhou, Cen, Tian, Wang, & Zhang, 2019). Volatiles from resistant cultivars contain volatiles that can directly inhibit pathogen growth or induce systemic resistance in neighbour susceptible cultivars (Lazazzara et al., 2018; Quintana-Rodriguez et al., 2015). Inter-plant signals can suppress plant pathogens directly or indirectly through microbiome adaptation. Intercropping of aerobic rice and watermelon reduces disease severity of *F. oxysporum* in watermelon (Ren et al., 2008). Rice root exudates reduce pathogen spore germination up to 41% and alter the root microbiome community structure in favour 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 neighbouring 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 defence hormones and pathogenesis-related proteins in tomato, and reduces stem rot disease (Zhou et al., 2019).

Plant debris such as decaying organic matter or sloughed off root cells functions as a modulator and infochemical for the next plant generation and rhizosphere microbiome. 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 et al., 2019; Wang, Wu, et al., 2020).

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 neighbouring 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 *T. 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 defence. 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 et al., 2019). The formulation technologies and field applications of infochemicals is reviewed elsewhere (Sharifi & Ryu, 2018a, 2020).

4 | CONCLUDING REMARKS

Plants have adapted to growth in complex and competitive ecosystems during their evolutionary history. They need to compete with

interspecific and conspecific plants for light, water and nutrients, and communicate with neighbouring plants to anticipate upcoming biotic/abiotic challenges (Ballaré & Austin, 2019; Effah, Holopainen, & McCormick, 2019; Hodge, Fitter, & Robinson, 2013; Hortal et al., 2017). However, only some of the competition and communication 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 et al., 2015; Sharifi & Ryu, 2018c). The plant holobiome leverages the collection of its member genes to optimize performance and survival. Plants have spatiotemporal layers of defence consisting of rhizosphere microbes, endophytes, pattern-triggered immunity, effector-triggered immunity and recruited natural enemies; each of these can efficiently suppress specific groups of attackers (Carrión 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.

Information and signal transferring systems play important roles in plant growth and survival. Plants decipher their complex habitat situations by perceiving physical and chemical cues and signals, either directly from neighbouring plants or indirectly from their symbionts such as mycorrhiza, endophytic fungi and dodder. Previous research has characterized the signal types and signal mediators involved in plant interactions with other members of the ecosystem and revealed that deaf and mute mutants of plants have reduced ecological competence. However, plants may have lost some of their communication abilities during domestication and plant breeding programs. Therefore, plant breeders and genetic engineers should have a holistic view of plants as members of the holobiome. Otherwise, small changes in genes related to inter-plant and inter-kingdom signals may substantially affect plant performance, a phenomenon called the butterfly effect.

Agricultural practices also affect plant–plant communication. As we mentioned above, no-tillage and minimum tillage systems preserve common mycorrhizal networks and endophytic fungi as mediators of wired plant–plant communication. Moreover, Information can transfer between plants during intercropping or from crop to crop in the next season. Thus, recent advances in our understanding of plant–plant communication can help manage agricultural practices so that they utilize the abilities of plants to exploit ecological interactions, and survive in competitive environments.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

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