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PERSPECTIVE



Integrating plant-to-plant communication and rhizosphere microbial dynamics: ecological and evolutionary implications and a call for experimental rigor

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The perception of airborne chemical signals by plants can trigger reconfigurations of their metabolism that alter their biotic interactions. While plant-to-plant chemical communication has primarily been studied in the context of eliciting defenses to herbivores and pathogens, recent work suggests that it can also affect plants' interactions with their rhizosphere microbiomes. In this perspective, we discuss the potential for integrating the fields of plant-to-plant communication and microbial ecology to understand the chemical ecology of plant–microbiome interactions. As an introduction for microbial ecologists, we highlight mechanistic knowledge gaps in plant volatile organic compound (VOC) perception and provide recommendations for avoiding common experimental errors that have plagued the plant communication field. Lastly, we discuss potential implications of plant VOCs structuring rhizosphere microbiomes, particularly effects on plant community and evolutionary dynamics. As we continue to discover links between plant metabolism and their microbiomes—from molecular to community scales—we hope that this perspective will provide both motivation and words of caution for researchers working at the intersection of these two fields.

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INTRODUCTION

Few topics in plant biology have intrigued scholars as much—or been as controversial—as plants' ability to exchange information about their changing environments through chemical cues. Yet, while the “talking trees” phenomenon is now widely accepted, many questions remain about how and why these chemical conversations occur, and how they impact ecological processes. In the most well-studied examples, plants emit distinctly altered volatile organic compound (VOC) bouquets in response to herbivore and pathogen attacks. Neighboring plants perceive these chemical cues and induce or ready their own direct defenses against the oncoming antagonist. These responses to a neighbor's stress cues have been largely interpreted as “eavesdropping” that mostly benefits the receiver of the information [1]. However, recent studies have found that this exchange of chemical information can also benefit the emitter through inclusive fitness when the receiving neighbors are related or through risk-sharing when information exchange promotes a more even distribution of damage throughout the population [2, 3]. While these studies suggest that antagonists can function as agents of selection on the emission (and perception) of induced VOCs, many questions remain regarding the underlying mechanisms and ecological relevance of VOC-mediated plant communication.

While plant-to-plant communication research has historically focused on the role of VOCs in triggering responses to specific herbivores and pathogens, volatile communication may also play a much broader role in shaping plant–microbe interactions, which

mainly play out in the rhizosphere. Both beneficial and pathogenic microbes are powerful agents of selection on plants and can alter plant phenotypes in a myriad of ways [4]. However, the extent to which plants are capable of functionally shaping their own microbiomes remains unclear. It is known that rhizosphere microbial communities can be measurably altered by phytohormones and other plant metabolites present in soils [5–7], and that these exudates are, in turn, affected by VOC-mediated plant-to-plant communication. Moreover, plant-associated microbes themselves emit a diverse array of VOCs which can directly affect the metabolism of plants [8] or other microbes. While VOCs emitted by both plants and microbes have been shown to affect plant resistance to specific pathogens, their effects on the broader composition of plant-associated microbial communities have rarely been investigated. However, pioneering studies on *Arabidopsis thaliana* suggest that rhizosphere microbial communities can be affected by plant innate immune responses to pathogens [6].

A recent study by Kong et al. (2021) has begun to build this bridge between plant-to-plant VOC communication and rhizosphere microbial ecology. The researchers suggest that microbe-induced leaf VOC emissions can restructure the rhizosphere microbiomes of neighboring plants [9] (Fig. 1A). In their key experiment, they exposed tomato plants growing in autoclaved soil to conspecifics inoculated with a common plant-growth-promoting rhizobacterium (PGPR), *Bacillus amyloliquefaciens*, in an enclosed chamber, which allowed aboveground airflow but no connections through the soil. They found that the rhizosphere

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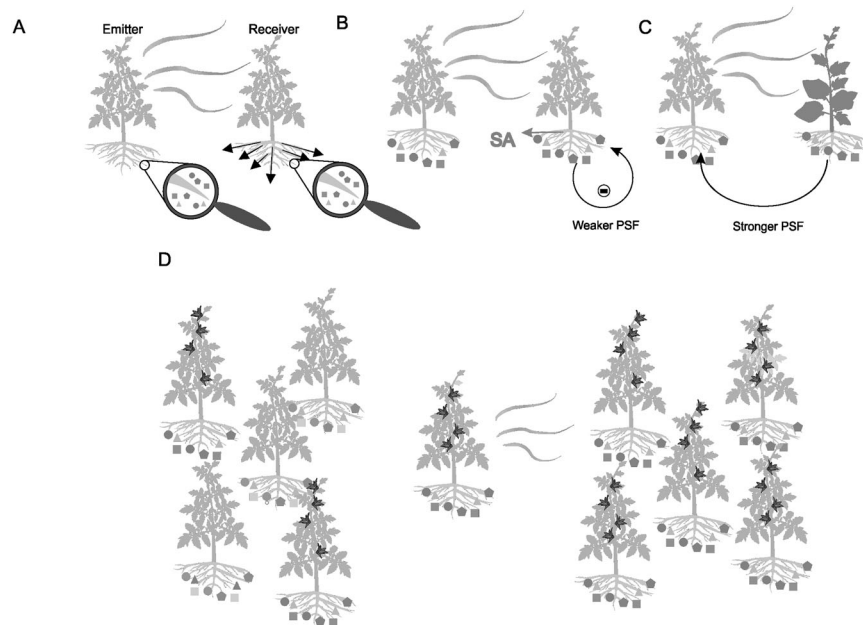


Fig. 1 Ecological and evolutionary consequences of VOC-mediated rhizosphere effects. In the mechanism proposed by Kong et al. (2021) (A), microbe-induced plant VOCs synchronize the rhizosphere microbial communities of neighboring plants through changes in plant metabolism (e.g., salicylic acid (SA) exudation) [9]. These metabolic and rhizosphere microbial effects may affect plant community dynamics by altering microbially-driven plant-soil feedbacks (PSFs). For example, SA-driven shifts in rhizosphere communities may reduce species-specific pathogen loads that contribute to negative (inhibitory) PSFs amongst conspecific plants (B). Conversely, rhizosphere homogenization between heterospecific plants could potentially strengthen PSFs (e.g., exacerbate negative PSFs if similar microbial communities tend to be inhibitory) (C). Rhizosphere homogenization among neighboring plants may also beget local synchronization of microbially-mediated traits such as flowering time (D). Here, plants downwind of the emitter-plant flower synchronously (right), while the plants upwind maintain variation in their microbiomes and phenology (left). This synchronization could reduce phenotypic variation within plant populations, potentially reducing opportunities for natural selection to act on these traits.

bacterial communities of these plants became more similar to those of the inoculated plants to which they were exposed. It is widely recognized that PGPRs exert their beneficial effects on plant growth, at least partially, by reducing pathogen pressure through the modulation of plant innate immunity [7]. However, this is the first study to show that PGPR-mediated immune-priming can spread to neighboring plants through volatile plant-to-plant communication.

Through a series of experiments, they then elucidated the microbe-induced production of a common plant VOC, β -caryophyllene, as a driver of changes in root exudation, and consequent rhizosphere bacterial interactions, in the exposed plants. Thus, they not only presented a proof-of-concept for a novel mechanism of rhizosphere synchronization (Fig. 1A), but also identified a putative mechanism of the airborne plant-to-plant transfer of information, as well as changes in plant metabolism that could affect plant–microbe interactions in the rhizosphere [9]. However, this study also highlights a common major flaw in plant-to-plant communication research, as well as important gaps in our mechanistic understanding of plant chemical perception. In this perspective, we provide suggestions for how the field should move forward to address these shortcomings while discussing the potential ecological and evolutionary implications of VOC-mediated rhizosphere synchronization.

Building a strong foundation for plant-to-plant VOC communication research

The phenomenon of plant-to-plant chemical communication has been met with skepticism due to both problematic experimental designs and missing links in our understanding of plant chemical perception. Here we review these issues, providing suggestions for designing plant VOC exposure experiments and using the mechanisms proposed by Kong et al. (2021) to highlight current

knowledge gaps in our general mechanistic understanding of VOC perception [9].

Independently replicated and realistic experimental designs. Early plant communication experiments faced widespread criticism in the scientific community due to the lack of appropriate replication [10]. However, previous attempts to point out these experimental design failures have only been partially successful in reducing the incidence of pseudoreplication in published studies on plant-to-plant communication. This new study [9] is, unfortunately, no exception. Due to the pseudoreplicated design of their key experiment (apparently all four replicates of each treatment were tested within the same chamber, as in Fig. 2A), the study cannot actually rule out the possibility that the induced similarities between rhizosphere microbiomes are caused by simple chamber effects [9]. Experiments with true independent replicates are particularly crucial for laboratory studies of VOC-mediated communication where chamber effects are expected to be high. Independent replication in these types of experiments can be accomplished by pairing replicate emitters and receivers in individual chambers (Fig. 2B). In microbial experiments, inadvertent contamination of the chambers is an additional factor that could easily lead to large chamber effects that are unrelated to the planned treatments. Another common source of pseudoreplication (common in both laboratory and field experiments) is the exposure of multiple plants to the same emitter. While pseudoreplication has been widely recognized as a problem in plant-to-plant communications studies [10], similar concerns have been raised more recently about the common practice of inoculum pooling in soil microbiome studies [11]. Thus, as researchers begin to explore this intersection of plant-to-plant communication and microbial ecology, they should carefully consider statistical issues arising from pseudoreplication when

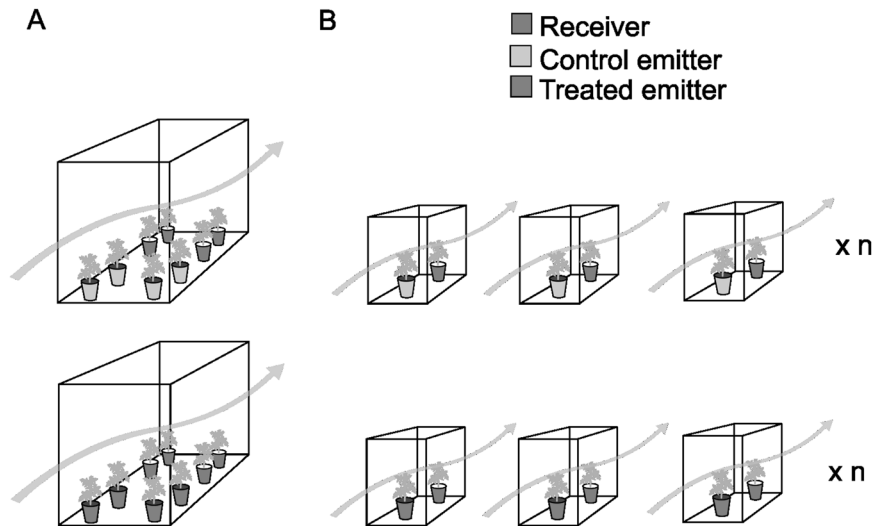


Fig. 2 Comparison of pseudoreplicated (A) and independently replicated (B) plant-to-plant VOC communication experimental set-ups. In an experiment exploring the effects of a treatment (e.g., inoculation with a beneficial microbe in Kong et al. (2021)) on VOC-induced responses in neighboring plants, “receiver” plants are exposed to treated or untreated control “emitter” plants in enclosed chambers with controlled airflow [9]. In a pseudoreplicated design (A), all replicate receiver plants of each treatment group are exposed within the same chamber, such that the treatment effects are confounded by potential chamber effects. In contrast, independently replicating chambers within each treatment group (B) allows researchers to distinguish the effects of the treatment from chamber-based variation.

designing experiments.

In addition to ensuring that experiments are statistically sound, researchers should also consider the ecological realism of their designs. While laboratory chamber trials are appropriate for proof-of-concept studies like Kong et al. (2021), they do not reflect the complexity of agricultural fields or natural plant communities [9]. In enclosed chamber experiments, plant VOCs from emitters build up within the chamber or are forced to flow unidirectionally towards a receiver, such that the receiver is often exposed to unrealistically high doses of VOCs compared to natural environments where VOCs disperse freely in the air and interact with VOCs emitted by neighboring plants. While environmental variables that can affect the dispersal of VOCs such as temperature and relative humidity can be controlled in laboratory chambers to mirror natural field conditions, chamber experiments typically do not accurately reproduce the atmospheric conditions (e.g., turbulence, UV radiation, and background composition of potentially-interfering VOCs) associated with natural environments. Carrying out such experiments in open field conditions or outdoor screen houses (where soil microbes could still easily be manipulated and sampled in pots) could help researchers assess the relevance of VOC-mediated communication in agricultural and/or natural settings and ask broader ecological and evolutionary questions.

Mechanistic understanding of VOC perception and downstream effects on the rhizosphere. Whereas airborne phytohormone derivatives are perceived by known receptors [12], the mechanisms of perception of other VOCs involved in plant-to-plant communication remain obscure. Understanding the molecular mechanisms of VOC perception would greatly facilitate studies assessing the ecological and especially the evolutionary significance of plant VOC-mediated information transfer. Three basic mechanisms for VOC perception by plants have been proposed: (a) transduction through binding of VOCs to specific receptors, (b) transduction through interactions with cell membranes creating membrane potentials, and (c) the uptake and conversion of VOCs into compounds involved directly in defense [13]. While there is limited evidence for all three of these mechanisms, their relative importance and the extent of signal integration between them are poorly understood. The discovery of VOC receptors or other traits

relevant to VOC perception would open many new avenues of investigation into the ecological functions of VOC-mediated information transfer, especially in field experiments where it is exceedingly difficult to control or even estimate the exposure of experimental plants to environmental VOCs. For example, researchers could generate mutants impaired in VOC perception, measure selection on these traits in microevolutionary studies, or analyze macroevolutionary patterns of interspecific variation in VOC perception and signal transduction.

β -caryophyllene, the VOC implicated in Kong et al. (2021) as the mechanism of VOC-mediated rhizosphere restructuring [9], is a common sesquiterpene, occurring frequently both as a floral volatile as well as a damage-associated cue in a variety of plant species. Several previous studies on plant-to-plant communication have associated it with the induction of metabolic changes in neighboring plants. While the precise mechanism of these effects is still unknown, a transcriptional regulator was identified in a recent study that binds strongly to caryophyllene derivatives and, which may function as a receptor [14]. Interestingly, it belongs to the TOPLESS family of transcriptional corepressors which are key regulators of the jasmonic acid (JA), brassinosteroid, and auxin phytohormonal pathways.

As the mechanisms of plant VOC perception come into clearer focus, one of the most pressing questions is how VOCs interact with established defense-related phytohormonal pathways, such as the JA and salicylic acid (SA) pathways, and to what extent the mechanisms of perception and signal transduction of VOC signals are conserved amongst plant species. The JA, and especially SA, pathways are classically implicated in mediating induced responses to pathogen attacks [12]. With respect to the Kong paper, in particular, the involvement of SA is somewhat surprising, since other recent work has found that the response to β -caryophyllene was largely independent of SA in both *Arabidopsis thaliana* and *Nicotiana tabacum* [8, 14]. In *Arabidopsis*, the response to β -caryophyllene was JA-dependent [8], whereas it appeared to be at least partially independent of both major pathways in *N. tabacum* [14]. Since Kong et al. (2021) only measured phytohormone levels in root exudates, it is unclear to what extent the elevated levels of SA they observe are reflective of internal hormone titers [9]. While these results may be indicative of an induced defense response, as proposed by Kong et al.

(2021), SA may also have alternative functions in the root zone unrelated to its role in plant defense, such as the solubilization of soil nutrients [15] or as a carbon source for rhizosphere microbes.

While the increased exudation of SA in β -caryophyllene-exposed plants is intriguing, the authors do not present direct evidence that this is the mechanism of the observed effects on the composition of the rhizosphere microbiome. Prior work has found that osmotin, a protein expressed abundantly in roots and involved in pathogen defense (as well as osmoregulation), is strongly induced by β -caryophyllene treatment [14], providing an alternative, SA-independent mechanism through which induction by β -caryophyllene could shape rhizosphere communities. Here again, mutants can be a powerful tool to test hypotheses about the mechanisms of signal transduction. For example, SA and JA mutants have been used to investigate how these phytohormonal pathways are involved in the response induced by β -caryophyllene and other terpenoids [8]. If SA is involved, it would be important to know if it is functioning primarily (a) as a phytohormone (e.g., through effects on plant immunity), (b) as a carbon source for soil microbes, or (c) through some other mechanism (e.g., by influencing pH). These mechanisms could be partially disentangled by comparing mutants impaired respectively in SA production and perception. Future work should aim to investigate the mechanisms and specificity of changes in rhizosphere microbial composition engendered by VOC perception.

Functional analysis of rhizosphere changes. The accessibility of high-throughput sequencing has vastly improved our ability to describe taxonomic changes in microbiomes, but this information on its own tells us little about the functional significance of these microbial shifts. For example, while the phenomenon of VOC-induced rhizosphere synchronization is intriguing, its biological significance is unclear. Follow-up work should examine how plant VOC-induced changes in microbiomes affect host physiology and ecology by measuring traits related to plant performance and fitness (e.g., biomass, seed production) and/or important ecological interactions (e.g., pathogen or herbivore resistance). The functional characterization of these rhizosphere community changes is necessary to understand the broader ecological and evolutionary significance of plant-to-plant communication as discussed in the next section.

Ecological and evolutionary implications of VOC-mediated immune priming and rhizosphere synchronization

Studying VOC-triggered reshaping of rhizosphere communities [9] has great potential to advance our understanding of how microbes affect plant ecology and evolution. While the phenomenon was identified from single-strain inoculation experiments conducted in a simplified environment, its operation in natural plant communities could have profound effects on disease transmission and plant community and evolutionary ecology.

Potential effects on disease transmission and plant community dynamics. Growing evidence suggests that interactions with rhizosphere microbes can substantially influence the assembly of plant communities through so-called plant-soil feedbacks (PSFs) [16]. PSFs occur when plants condition soils in ways that facilitate (positive PSF) or inhibit (negative PSF) the growth of other plants growing (either concurrently or subsequently) in the same soil. Since negative PSFs are thought to be driven largely by the abundance of shared pathogens in soils [17], VOC-mediated immune priming (Fig. 1A) could be hypothesized to reduce negative PSFs by increasing the resistance of receiver plants (Fig. 1B). At the community level, VOC-mediated communication could drastically alter disease dynamics through the widespread synchronization of rhizospheres into immune-primed states. While prior work has recognized that induced immunity can structure rhizosphere microbiomes to increase pathogen resistance [6],

models suggest that airborne immune-priming can produce different ecological outcomes than the direct induction of defenses in plants [2]. Counterintuitively, some epidemiological models suggest that direct immune priming can result in cyclic population dynamics caused by the proliferation of individuals with partial immunity [18]. Thus, priming could potentially result in the increased proliferation of pathogens, even as it benefits individual host plants. These models suggest that not only the cost of infection, but also the efficacy, duration, and cost of priming can impact the size and frequency of the oscillations in pathogen populations. Systems involving multiple species of pathogens and/or host species could result in even more complex dynamics. Future theoretical and empirical work should address how VOC-mediated priming (as opposed to direct priming) would be expected to alter the expected outcome of these processes.

While Kong et al. (2021) suggest that plant VOCs can synchronize the rhizospheres of closely related neighbors (i.e., one tomato variety), a similar mechanism could operate between more genetically diverse, or even heterospecific, neighbors [9]. To begin understanding the generality of VOC-mediated rhizosphere effects, future research should investigate both the specificity of microbe-induced VOC emissions and VOC-induced changes in rhizosphere composition across plant species and genotypes, as well as with a diverse range of microbes. While predicting the outcomes of PSFs is a current challenge in plant ecology, previous research suggests that plant species with more similar rhizospheres are more likely to inhibit each other's growth through negative PSFs [16]. Thus, while rhizosphere synchronization could reflect increased host-control over the microbiome (presumably resulting in more positive PSFs), it could also be hypothesized to accentuate negative PSFs by contributing to the homogenization of the soil microbial community (Fig. 1C). It is also possible that synchronization could result in a fleeting benefit to the plant, followed by more negative long-term consequences due to the homogenization of the rhizosphere and/or the proliferation of primed, partially-immune types in the population. Further research will be necessary to determine what conditions would be most likely to promote each of these scenarios.

If VOC-mediated resistance reduces PSFs by interrupting disease transmission as hypothesized above, this could be a major new mechanism explaining the evolution of volatile communication, due to the clear collective benefit of halting the proliferation of shared pathogens. While the benefit of sharing information about herbivory appears to follow primarily from the distribution of damage more evenly between plants, communication about pathogens may have the potential to actually interrupt transmission entirely due to their lower mobility and lesser ability to exert informed host choice. On the other hand, theoretical models predict that the spread of partial immunity may actually increase disease prevalence as discussed above, so the outcome in each case would likely depend on the particularities of the pathosystem.

Potential effects on plant evolutionary dynamics. Aside from direct effects on disease dynamics, VOC-mediated rhizosphere restructuring could also affect plant evolution by altering selection on other microbially-influenced plant traits. As many aspects of plant phenotypes are modified by microbiomes [4], the synchronization of rhizosphere communities could reduce opportunities for natural selection to act on these traits by decreasing the overall level of phenotypic variation in a population. As Kong et al. (2021) demonstrated, rhizosphere microbes can influence the expression of plant secondary metabolites [9]. Such microbially-mediated effects on metabolism could be hypothesized to reduce the strength of selection on plant defensive traits if resistance is increased through a non-genetic mechanism. Flowering time is another ecologically and evolutionarily important trait that can be substantially influenced by microbial interactions [19].

Thus, microbial synchronization could beget phenological synchronization (Fig. 1D), altering interactions with pollinators and potentially limiting ecological speciation by preventing reproductive isolation. Alternatively, microbial effects could enhance divergence by concentrating gene flow within a locally-synchronized patch. As soil microbial communities may play an important role in mediating plant local adaptation [20], future studies should explore how VOC-mediated rhizosphere effects may affect plant evolutionary dynamics.

CONCLUSIONS

In conclusion, plant VOC-mediated rhizosphere synchronization is an intriguing phenomenon with many potentially important ecological and evolutionary implications for researchers to explore. With advances in our understanding of plant VOC perception and its integration with the rhizosphere, along with our rapidly increasing awareness of the importance of microbiomes in plant science, we believe that the bridge forged by Kong et al. (2021) will be heavily travelled [9]. But, as researchers embark on this path, we urge them to avoid repeating past mistakes from the field of plant-to-plant communication to ensure the field moves forward on a solid foundation.

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AUTHOR CONTRIBUTIONS

All authors conceived of the idea and developed content and structure for this paper. MMH wrote the first draft. MMH and EB lead and coordinated the writing to which all authors contributed. AC developed and created the figures with input from all authors.

COMPETING INTERESTS

The authors declare no competing interests.

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