



Specificity and context-dependency of plant–plant communication in response to insect herbivory

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Over three decades of work on airborne plant communication have taught us that plants send, receive, and respond to volatile organic compounds (VOCs) emitted by conspecific as well as heterospecific neighbouring plants. Much of this research has focused on the consequences of plant–plant communication on resistance against herbivory, with studies showing that VOCs emitted by herbivore-damaged plants increase resistance of neighbouring undamaged plants. However, a key aspect that has received less attention concerns the ecological specificity and context-dependency of this phenomenon. Knowledge on this is crucial for assessing the ecological mechanisms that govern plant communication, determining its biological significance under natural conditions, as well as designing effective strategies for its application (e.g. in crop protection). Here we synthesize important advances from incipient work on the ecological specificity of plant communication according to three main aspects: plant-based specificity, herbivore-based specificity, and the influence of the abiotic context. We then provide some ideas for future research to improve our understanding of the specificity of plant communication and its ecological and evolutionary importance.

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Introduction

Plants emit complex blends of volatile organic compounds (VOCs), including green leaf volatiles, nitrogen-containing compounds, and aromatic compounds [1,2^{*},3]. These airborne compounds are produced constitutively or can be induced in response to biotic and abiotic

stimuli [4,5], and play diverse ecological functions such as: plant protection against extreme abiotic conditions (e.g. thermo-tolerance [4]), attraction of insect pollinators and seed dispersers [6–8], indirect plant defence by attracting arthropod predators or parasitoids of herbivores [9–11], and plant-to-plant communication by acting as warning signals of herbivore presence to neighbouring plants [12,13].

Over three decades of work on airborne plant communication have demonstrated that plants emit and respond to VOCs emitted by conspecific [12,14–17] as well as heterospecific [18,19] neighbouring plants. Most of this work has centered on the consequences of plant–plant communication for resistance against herbivory, with studies showing that VOCs emitted by herbivore-damaged plants (emitter plants) increase resistance of neighbouring undamaged plants (receiver plants) [13]. Responses by receiver plants often involve priming or preparation of defensive responses (rather than full induction), which leads to enhanced defence induction upon subsequent insect attack [13,20]. Plant communication is thought to be widespread and an increasing number of studies have proposed the use of plant VOC-mediated signalling as an alternative for sustainable crop protection against pests and diseases [21–23]. For example, the exogenous application of VOCs mediating plant communication could be used to prime plants and increase pest resistance [22], representing a complementary (and potentially synergistic) approach to applying plant hormones to enhance direct and indirect plant resistance [24,25].

Despite promising findings, the ecological and evolutionary significance of VOC-mediated plant communication has been questioned primarily on the basis of the ephemeral nature of these compounds and their localized range of action [1]. It has been argued that VOCs serve mainly physiological roles and that their release is an unavoidable consequence of their physiochemical properties (e.g. high volatility [12]). However, the fact that plants have developed biochemical mechanisms to receive and interpret these signals indicates a role of these compounds that is beyond solely a by-product of direct defensive mechanisms [2^{*}]. With this in mind, two non-mutually exclusive hypotheses has been posed to explain the ecological and evolutionary role of plant communication. One of these invokes kin selection as a mechanism for the origin and maintenance of plant communication among conspecifics [26^{**},27], whereas the other argues that this phenomenon functions essentially as a within-plant signalling

mechanism that triggers the induction of different plant parts without the need for internal connections between them [28,29]. To date, the relative importance of these two mechanisms remains unresolved, pending on the one hand on future laboratory-based studies that identify the biochemical mechanisms of release and reception of VOCs, and on the other on field-based work measuring concentrations of VOC emissions and consequences for plant fitness under realistic ecological settings [2*].

Based on the current state of the field, a key aspect that has received little attention concerns the ecological specificity and context-dependency of plant communication. Identifying the underlying molecular and biochemical mechanisms of plant communication has been considered a top research priority [2*], whereas aspects related to the specificity of plant communication in relation to the players involved (i.e. plants and associated insects) and its contingency upon biotic and abiotic factors under natural settings have been seldom discussed. This information is critical for moving beyond describing the presence or magnitude of plant communication, to assessing the ecological mechanisms that govern this phenomenon, its biological significance under natural conditions, and designing effective strategies for its use in crop resistance. Here we synthesize the most important findings from recent work on the ecological specificity of plant communication under three perspectives: plant-based specificity, herbivore-based specificity, and the importance of the abiotic context as a source of variation in strength and specificity of this phenomenon. We end by providing ideas for future research on the specificity of plant communication.

Recent advances in the specificity of plant–plant communication

Plant-based specificity

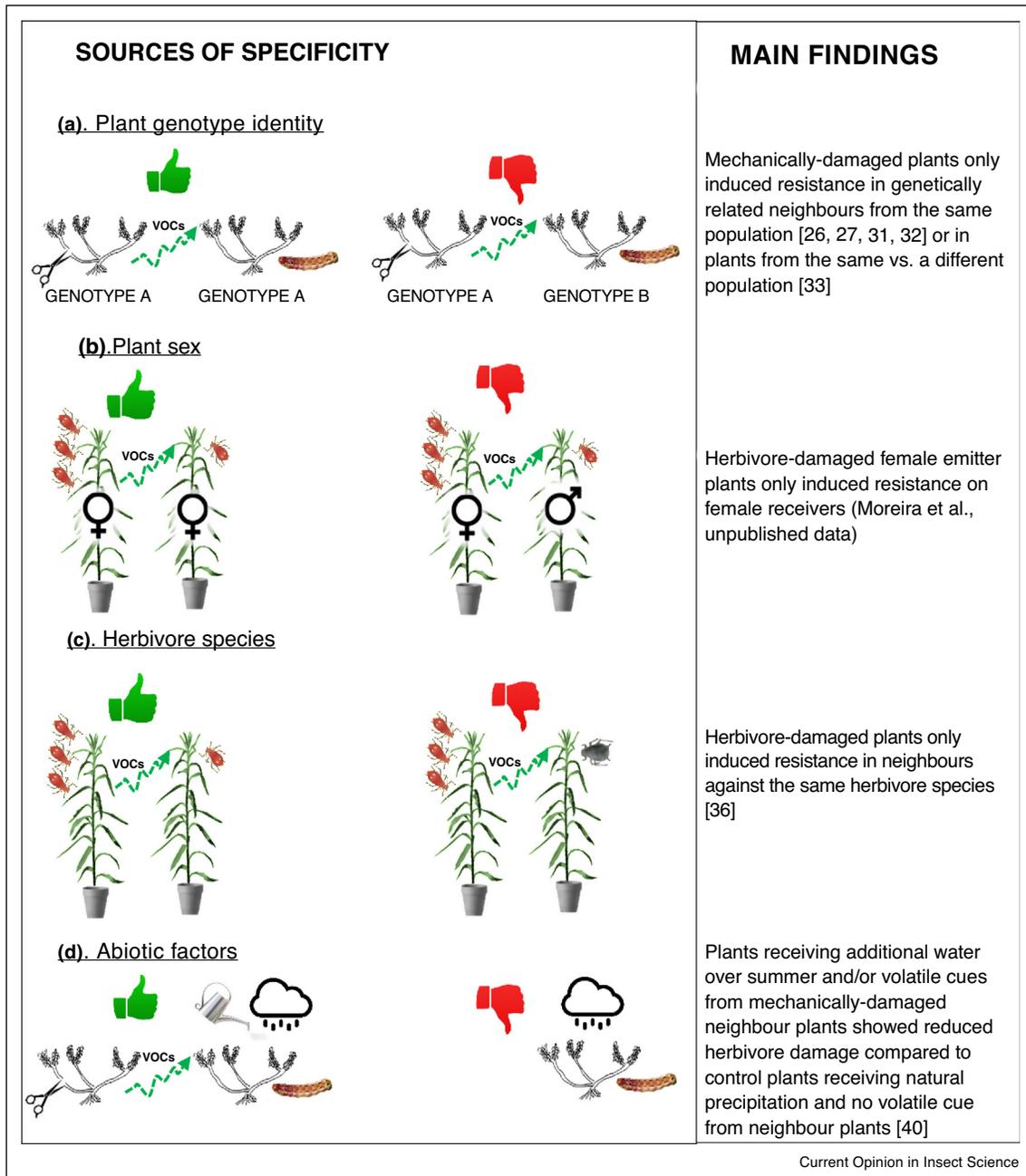
Recent work has demonstrated that communication is contingent on the plant's genotype identity. Evidence for this plant-based specificity come mostly from research by Karban and collaborators with sagebrush (*Artemisia tridentata*). Notably, they found that sagebrush receiver plants responded more strongly to volatile cues from mechanically damaged emitter plants that were genetically related to them than to VOCs from unrelated emitter plants (Figure 1a) [26**,27]. Because communication between unrelated individuals should be costly for emitter plants as it would increase a competitors' fitness at the expense of its own [30], one explanation for this phenomenon is that kin selection favours effective communication among groups of closely related plants. Similarly, in another study they reported that VOCs emitted by damaged sagebrush plants separate into two heritable chemotypes (dominated by either thujone or camphor) [31]. The identity of the emitting plant chemotype had important consequences for plant communication because, following leaf damage to emitter plants, receiver

undamaged plants of the same chemotype as the emitter plant exhibited greater induced resistance relative to receivers of a different chemotype than the emitter [31]. More recently, they also found that VOCs emitted by sagebrush plants vary geographically and reciprocal transplants across populations demonstrated that plants communicated more effectively with local than non-local neighbours (Figure 1a) [32*]. Accordingly, recent work with other plant species has reported similar findings. For example, Moreira *et al.* [33*] found that lima bean (*Phaseolus lunatus*) plants exhibit population-specific 'dialects' such that only receivers from the same source population as the damaged emitters suffered less leaf damage upon exposure VOCs (Figure 1a). Likewise, Pettersson *et al.* [34] found that attraction of the aphid *Rhopalosiphum padi* to barley (*Hordeum vulgare*) plants was reduced more strongly when plants were previously exposed to VOCs from emitter plants of the same cultivar relative to when they received VOCs from emitters of a different cultivar. Overall, evidence for genetically-based plant variation in communication remains scarce, but as more studies accrue a clearer picture will emerge as to the presence and magnitude of plant genetic variation in both VOC emission and reception (i.e. variation in emitters and receivers). Detecting significant variation is a necessary pre-requisite to test the evolutionary significance of this form of plant communication.

Plant sex appears to be another important source of specificity in communication (Figure 1b). Genetically-based sexual dimorphism in plants has been reported for growth-related and resistance-related traits [35], and might also involve differences in VOC emissions. Accordingly, recent work found that communication in the dioecious *Baccharis salicifolia* is contingent on whether emitter and receiver plants are of the same sex. Volatiles from male emitter plants induced resistance in both male and female receivers (Figure 2a), whereas those from female emitter plants only induced herbivore resistance on female receiver plants (Figure 2b) (Moreira *et al.*, unpublished data). This sex-determined asymmetry in communication appears to be explained by differences in the relative amounts of VOCs induced by herbivore feeding. Specifically, the induction of pinocarvone was five-fold greater in female than in male plants, suggesting that this compound played a role in mediating the observed specificity in female plant communication.

The above findings indicate plant genetic variation in communication-related VOCs, particularly that plant relatedness and sex represent important sources of variation determining the efficacy of this phenomenon. Previous findings suggest that VOC emissions are under selection to increase plant fitness by involving benefits for groups of related plants with shared herbivores as a mechanism explaining the origin (or at least maintenance) of airborne

Figure 1



Summary of recent advances on the ecological specificity of plant communication based on plant-based (genotype and sex) specificity, herbivore-based specificity and the importance of abiotic context.

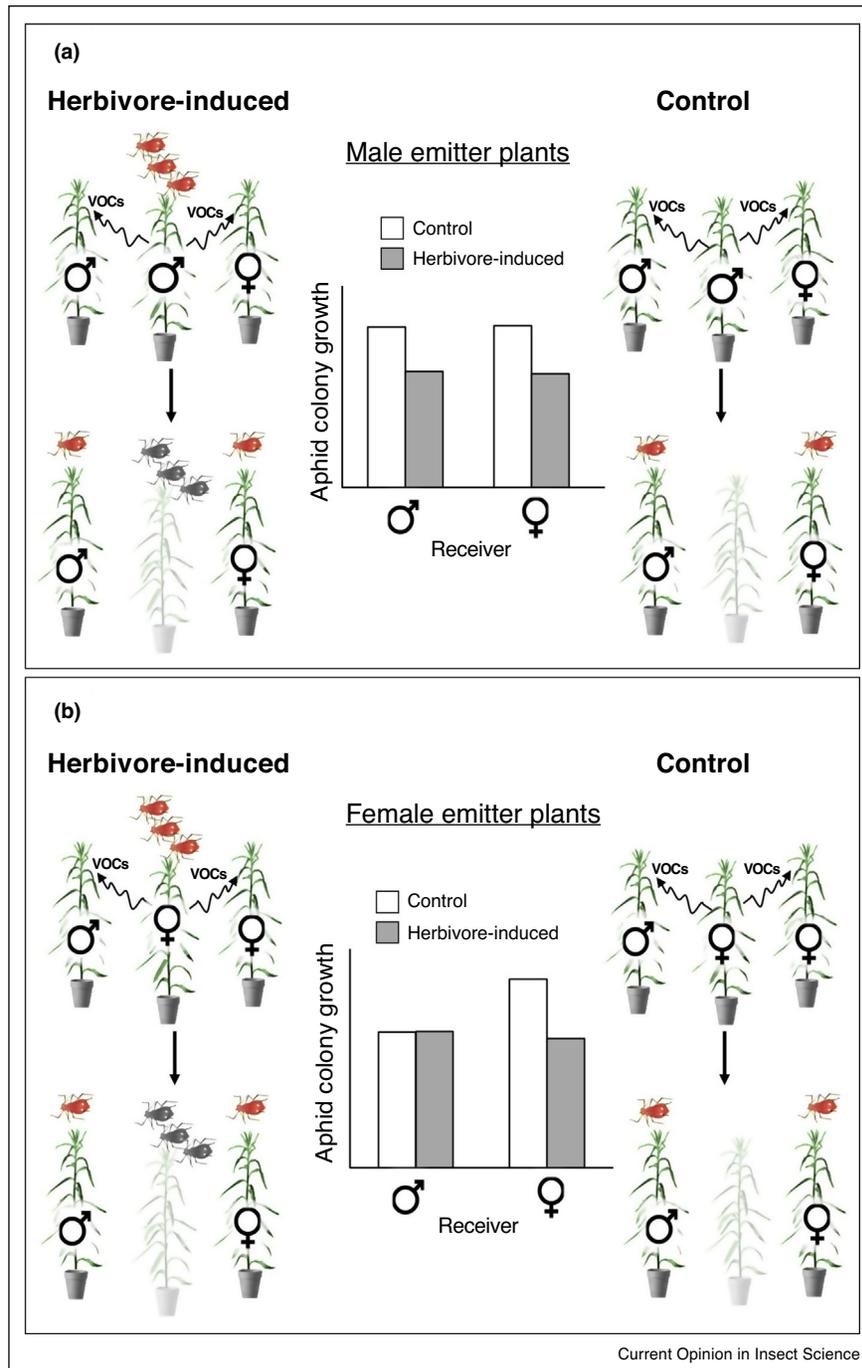
plant communication (but see Ref. [2^{*}]). Alternatively, results also suggest that eavesdropping by neighbouring plants using within-plant signalling processes is more effective between related plants or plants of the same sex because they share a greater similarity in VOC emissions.

Herbivore-based specificity

Recent work of ours with *B. salicifolia* and two aphid species has shown that plant communication is highly

dependent on the identity of the attacking herbivore. We found that each aphid species induced a different composition of VOCs in emitter plants, which was in turn associated with differences in induced resistance by undamaged receiver plants exposed to VOCs from each group of emitters [36^{**}]. Notably, induced resistance in the receiver plant was specific to the identity of the herbivore feeding on the emitter plant: induced resistance in receiver plants only occurred when emitter and

Figure 2



Depiction of experimental design used to test for effects sex-based specificity in plant communication on resistance to the specialist aphid *Uroleucon macolai* in the dioecious *Baccharis salicifolia*. Panel (a) shows the portion of the experiment used to test for effects of aphid induction of male emitter plants, whereas Panel (b) shows the test of effects of aphid induction of female emitters. In both cases, treatments involved measurements of aphid colony growth (i.e. proxy of reproductive success) on both male and female receiver plants exposed to VOCs from non-induced (control) or herbivore-induced emitter plants (white and grey bars, respectively). Overall, results indicated that aphid reproduction was significantly lower on both male and female receivers exposed to VOCs from induced relative to control male emitters, whereas exposure to VOCs from female emitters significantly reduced aphid reproduction on female but not male receivers.

receiver plants were attacked by the same aphid species (Figure 1c) [36**]. This pattern of specificity makes sense from an adaptive perspective in that receiver plants are inducing responses that are tailored to the herbivore attacking neighbouring plants, and this specificity is presumably determined by specific volatile blends or compounds.

Herbivore specificity in plant communication is presumably due to the differential induction of particular VOCs. In the case of *B. salicifolia*, the total amount or relative abundance of compounds such as (E)- β -ocimene, limonene, nonatriene, and pinocarvone found in VOC blends differed depending on the aphid species feeding on the plant [36**]. These findings suggest that VOCs released by plants upon insect damage could parallel the well-reported specificity of induced direct defences [37,38]. In addition, the emission of VOCs mediating plant communication is likely also shaped by herbivore-specific variables such as elicitors in oral secretions and by the intensity and pattern of damage, as has been shown for VOCs involved in indirect resistance [5,39]. Despite these promising findings, further research with other herbivore guilds (e.g. chewers, miners) is needed in order to understand the commonness, causes, and consequences of herbivore specificity in plant–plant communication.

Abiotic factors and the specificity of plant communication

Abiotic conditions can influence plant volatile emissions, and therefore represent a potentially important source of variability in plant communication. To our knowledge, only one study to date has tested for abiotic context-dependency in plant communication. In this study, Pezzola *et al.* [40**] reported that sagebrush plants receiving additional water over summer, volatile cues from mechanically-damaged neighbouring plants, or both showed reduced herbivore damage compared to control plants receiving natural precipitation and no volatile cues from neighbours (Figure 1d). There was no evidence, however, of interactive effects of water and emitter VOCs on receiver resistance, suggesting that the strength of induced resistance from exposure to VOCs in receivers was not contingent on water availability. The authors discuss that water availability directly boosts resistance to herbivory (either through increased constitutive or induced defences), and that responses to VOCs may be an important resistance mechanism under water-limited conditions. It would be useful to address the effects of water availability on the amount and composition of emitter VOCs, to test for abiotic effects not only on receivers but also on the volatile cues produced by emitters.

Although we do not know much about abiotic controls over plant communication, related studies indicate that abiotic context-dependency might be common. For example, some studies have found strong effects of

warming, CO₂ enrichment, and water availability on VOC emissions under the context of plant indirect defence (reviewed by [4,41]). Similarly, field studies along ecological gradients have found patterns suggestive of abiotic controls (e.g. resource availability and temperature) on the inducibility of plant VOCs [42,43]. To the extent that such changes in VOC emissions also influence plant communication [23], these studies imply that abiotic variation must be considered in building a robust paradigm on the specificity of plant–plant communication.

Outlook and challenges for future work

An understanding of the biochemical mechanisms of VOC emission and reception as well as the ecological factors influencing plant communication is necessary to explain and predict the specificity and context-dependency of this phenomenon. We next focus on several key challenges and opportunities for the next decade of research, namely: first, identifying key VOCs and understanding their multiplicity in ecological roles, second, achieving a better understanding of communication dictated by herbivore-based specificity, and third, addressing the extended, community-level consequences of plant communication.

There is a pressing need to identify VOCs with disproportionately large effects on receiver plants, and to understand how qualitative and quantitative changes in VOC blends determine the strength of effects on receivers and the specificity of plant communication. In addition, many of these compounds are involved not only in communication but also serve to attract natural enemies of herbivores or plant mutualists. Understanding their ecological function thus requires addressing the roles of VOCs under different interaction contexts (e.g. plant–plant, plant–herbivore, plant–pollinator) or degrees of trophic complexity (e.g. plant–herbivore versus plant–herbivore–predator). A greater integration of research on the role of specific VOCs in plant indirect defence and plant–plant communication will be highly beneficial for identifying common underlying VOCs and mechanisms.

Special attention to herbivore-based variation in plant communication is also needed, including the mechanisms underlying variation in communication depending on herbivore traits such as feeding guild or diet breadth. For instance, it would be interesting to investigate whether previously reported herbivore or pathogen interactions mediated by plant induced direct defences (e.g. cross-talk between plant defence signalling pathways) also extend to VOC-mediated interactions under the context of plant–plant communication. Specifically, future studies could address whether guilds of insect herbivores associated with a given plant defensive pathway induce VOC blends that predictably decrease or enhance induced resistance on receiver plants attacked by insect guilds associated with a different pathway.

The recognition that plant–plant communication can influence not only plant–herbivore interactions, but also other members the community, is a key aspect to consider in future work. For example, exposure to VOCs from damaged plants may induce not only direct but also indirect defences in receiver plants. Enhanced direct defences in receiver plants may affect the third trophic level indirectly via effects on herbivore abundance or traits (e.g. foraging behaviour), whereas induction of VOCs may directly influence predator abundance and behaviour. In either case, communication can lead to an alteration of multi-trophic interactions associated with receiver plants which may in turn influence subsequent communication events among neighbouring plants. Assessing how communication influences the extended community, the occurrence of feedbacks, and the different pathways through which such effects take place will yield insight into the ecological relevance and net effects of plant communication on plants themselves and associated insects.

Evaluating the above aspects of plant communication under realistic ecological settings is needed, from mesocosms and common gardens to tractable manipulations in natural plant patches or stands. These undertakings should also consider manipulations of relevant abiotic factors to test for context-dependency in plant communication. In addition, the role of plant cues in mediating below-ground plant interactions [44] and the influence of microbes in shaping plant volatile-mediated interactions [45] are active lines of research in plant–insect interactions which can be addressed within the context of plant communication. A promising future lies ahead for research on plant communication, one where we move closer to understanding the ecological and evolutionary significance of this phenomenon, as well as apply this knowledge to design environmentally sound strategies to boost crop protection against pests.

Conflict of interest statement

Nothing declared.

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