

Explaining evolution of plant communication by airborne signals

Martin Heil¹ and Richard Karban²

¹ Departamento de Ingeniería Genética, CINVESTAV - Irapuato, Km. 9.6 Libramiento Norte, CP 36821, Irapuato, Guanajuato, México

² Department of Entomology, University of California, Davis, CA 95619, USA

In spite of initial doubts about the reality of ‘talking trees’, plant resistance expression mediated by volatile compounds that come from neighboring plants is now well described. Airborne signals usually improve the resistance of the receiver, but without obvious benefits for the emitter, thus making the evolutionary explanation of this phenomenon problematic. Here, we discuss four possible non-exclusive explanations involving the role of volatiles: in direct defense, as within-plant signals, as traits that synergistically interact with other defenses, and as cues among kin. Unfortunately, there is a lack of knowledge on the fitness consequences of plant communication for both emitter and receiver. This information is crucial to understanding the ecology and evolution of plant communication via airborne cues.

Communication among plants: facts, artifacts and problems of acceptance

Plants are dumb and deaf, and plant communication runs counter to human common sense. As a consequence, it was not until the early 1980s that the first reports on ‘talking trees’ entered the scientific literature. In 1983, Sitka willow (*Salix sitchensis*) growing close to herbivore-infested conspecifics were reported to express higher levels of resistance to herbivores than did plants that were growing further away [1]. Similarly, undamaged poplar (*Populus x euroamericana*) and sugar maple (*Acer saccharum*) saplings increased their anti-herbivore defense when exposed to the air around damaged, resistance-expressing plants [2]. It was postulated that the attacked plants had ‘warned’ their neighbors.

However, an interaction in which plants increase the fitness of their neighbors without improving their own fitness results in an evolutionary disadvantage for the emitter, and therefore represents ‘eavesdropping’ rather than true communication (see Glossary). Although the initial reports were heavily criticized for this and other reasons [3], the phenomenon undoubtedly exists: volatile organic compounds (VOCs), which are released from resistance-expressing plants, can trigger specific defensive responses in neighboring plants of various species (Table 1). Most of the underlying physiological and genetic mechanisms remain to be discovered, but several studies have demonstrated that plants growing in nature can benefit from a VOC-mediated resistance expression [4–6].

A particularly pertinent problem for future research into plant communication is the lack of empirical data

on the consequences of this phenomenon on the fitness of the emitter. This knowledge is crucial to the understanding of the evolutionary origin and consequences of plant communication by airborne signals. Here, we discuss how novel empirical findings and existing theoretical models can be merged to formulate concrete questions and plausible, non-exclusive explanations for the evolutionary onset and maintenance of plant defense induction by volatile cues. Plants respond with induced resistance to attack by pathogens or herbivores [7,8]. Because pathogens and herbivores are mobile, such responses are usually expressed systemically, that is in healthy organs of the attacked plant. Although several vascular long-distance signals can mediate this phenomenon, within-plant signaling is also triggered by volatile cues [4,9–11]. Given that VOCs are released from the surface of the plant, their effects are not restricted to the emitting plant but can

Glossary

Allelopathy: the inhibition of the germination or the development of plants by chemical compounds that are released from roots or aerial parts of neighboring plants.

Cheaters: exploiters of mutualistic interactions that have evolved from former mutualists and that make use of the information or other types of resource produced by one partner without rendering any mutual benefit [87].

Eavesdropping: the act of listening surreptitiously to a private conversation. Here, the term refers to the perception of information from an emitter by a receiver that does not return a benefit to the emitter.

Extrafloral nectar (EFN): nectar involved in the indirect defense of plants via the attraction of ants and other predatory arthropods [73]. EFN secretion can be induced by herbivory and by exposition of plants to herbivore-induced VOCs and is not involved in pollination.

Green-leaf volatiles (GLVs): small C₆ volatile compounds (mainly alcohols and aldehydes) that are formed from pre-existing lipid precursors by pre-existing enzymes in response to plant tissue disruption. GLVs are released within seconds from physically damaged plants [88]; they form the typical odor of freshly mowed grass.

Inclusive fitness: the combination of direct and indirect fitness components; ‘direct fitness’ describes the impact on the fitness of an individual that results from its own reproduction and ‘indirect fitness’ comprises any impact on the fitness of its kin that carries the same genes.

Kin selection theory: explains the evolutionary stability of altruistic behavior by beneficial effects of the behavior on the inclusive fitness of an organism and predicts that to express altruistic behaviour individuals within a social group must be related to a higher degree than are two random individuals of the population [80].


Plant-plant signaling: results from cues that are emitted from a plant in a plastic and conditional manner and that cause rapid responses in a receiver. Whether this phenomenon can be termed ‘plant communication’ based on the current empirical knowledge depends on whether ‘communication’ is reserved for events that serve both the emitter and the receiver of the signal.

Volatile organic compounds (VOCs): organic compounds with high vapor pressure. Here, more specifically, VOCs are volatiles released from plants in response to herbivore damage, comprising GLVs and compounds such as aromates and terpenoids whose production requires induced gene expression.

Within-plant signaling: any signaling among different parts or organs of a genetically defined, individual plant.

Corresponding author: Heil, M. (mheil@ira.cinvestav.mx).

Table 1. History of research on airborne plant–plant signaling

Year of first publication	Species		Induction of the emitter	Response induced in the receiver	Refs
1983	Willow (<i>Salix sitchensis</i>)		Natural herbivory	Resistance to natural herbivores	[1]
	Poplar (<i>Populus x euroamericana</i>)		Mechanical damage	Increased content of phenolic compounds	[2]
	Sugar maple (<i>Acer saccharum</i>)		Mechanical damage	Increased content of phenolic compounds	[2]
1990	Tomato (<i>Lycopersicon esculentum</i>)		Purified gaseous compounds released from sagebrush	Synthesis of proteinase inhibitors	[14]
1992	Cotton (<i>Gossypium hirsutum</i>)		Infestation with herbivorous mites	Increased attraction of predatory mites, reduced oviposition by herbivorous mites	[15]
1997	Tobacco (<i>Nicotiana tabacum</i>)		Infection with tobacco mosaic virus	Increases disease resistance	[16]
2000	Lima bean (<i>Phaseolus lunatus</i>)		Infestation with spider mites	Increased expression of defense-related genes	[17]
	Alder (<i>Alnus glutinosa</i>)		Manual defoliation	Increased resistance to natural herbivory	[19]
	Tobacco (<i>Nicotiana attenuata</i>)		Clipped sagebrush	Increased resistance to natural herbivory	[20]
	Bean (<i>Vicia faba</i>)		(Z)-jasmone identified as VOC released from several plant species	Increased synthesis of VOCs and attraction of predators	[28]
2004	Corn (<i>Zea mays</i>)		Caterpillar feeding	Priming of JA synthesis and VOCs release	[18]
	Barley (<i>Hordeum</i> spp.)		Intact thistles (<i>Cirsium</i> spp.) as emitter	Decreased attractiveness to aphids	[21]
	Sagebrush (<i>Artemisia tridentata</i>)		Clipped sagebrush	Increased resistance to natural herbivory	[89]
2008	<i>Arabidopsis thaliana</i>		Monoterpenes as released from herbivore-damaged plants	Changed expression of hundreds of genes	[26]
2009	Barley (<i>Hordeum</i> spp.)		Intact barley plants representing different cultivars as emitters	Decreased attractiveness to aphids and increased attractiveness to parasitoids	[23]

affect neighboring plants as well. Signaling among plants could therefore be evolutionarily derived from within-plant signaling. Clearly, future studies need to consider the consequences of interplant signaling on both the emitter and the receiver, and they will have to separate the consequences of VOC-mediated effects on neighboring plants from the multiple functions that VOCs exhibit in within-plant signaling and in other interactions of a plant with its abiotic and biotic environment (Box 1).

The history of plant communication research

The earliest descriptions of plant communication [1,2] were subject to alternative explanations, such as unex-

plored sources of mortality and pseudoreplication [12]. Following these critiques, most ecologists regarded communication among plants as a phenomenon that had been proposed, examined and debunked, somewhat akin to cold fusion [13]. However, these alternative explanations only suggested that the early evidence for plant communication was less than compelling, but not that the hypothesis had been disproved.

The next generation of experiments was more carefully designed [14–18] and convincingly showed that volatile signals are exchanged among plants. Because these studies were conducted in artificial laboratory settings, most ecologists doubted that similar phenomena could occur

Box 1. Outstanding questions

Although airborne signaling has become increasingly accepted, many questions remain. For example:

- Does the emitter benefit from plant–plant signaling? Depending on the definition of the term ‘communication’, this information decides whether the phenomenon is termed communication or eavesdropping. Although no positive fitness effects have yet been reported for the emitter, considering the community level provides attractive ideas: helping neighbors could reduce herbivore pressure at the population level and would improve the inclusive fitness of the emitter, particularly for species with short dispersal distances that have a higher probability of being surrounded by related conspecifics.
- How common is airborne signaling? This question needs to be answered both for the average plant in the field (is it normally induced, primed or uninduced?) and at the taxonomic level (which plant species respond to VOCs?).
- Is within-plant signaling the ‘raison d’être’ of VOC perception? If within-plant signaling is important, the capacity to perceive VOCs should be more pronounced in anatomically complex plants and in plants in arid habitats, where vascular communication is limited by plant–water relations.
- How common is within-plant signaling in relation to plant–plant signaling? The restricted distances over which volatile signals travel can significantly affect this ratio. Most organs exposed to VOCs emitted from a damaged leaf will normally form part of the same individual, and the probability of affecting only parts of the same plant increases with decreasing distances over which VOCs remain active.
- Is interspecific signaling the rule or the exception? Positive reports on interspecific signaling are restricted to two systems (Figure 1, main text): the effects of VOCs released from sagebrush on tomato and tobacco [14,20] and the effects of odors from thistle plants on barley [21]. Not all neighboring species responded [89], but we are not aware of other reports that excluded this possibility. Is sagebrush (an emitter of high amounts of MeJA) the exception, or does airborne plant–plant signaling generally cross species borders?
- How far does the signal travel? Distance is a crucial parameter, because volatiles diffuse in the air and move by eddy current dispersal. The distances over which VOCs can affect other plants therefore depend on abiotic factors, such as wind speed, air humidity and temperature.
- Do plants avoid auto-induction? VOCs-responsive traits include the emission of more VOCs. How can plants avoid a runaway process of reciprocal induction and autoinduction? Silencing by small RNAs and the observation that a ‘confirmatory’ attack is usually required for full induction [67] open possibilities for speculation. Future studies could use artificial VOCs and monitor the genetic, hormonal and biochemical changes in tissues of plants that have (or have not) been induced.

under natural conditions [12,13]. Several field experiments conducted during the 1990s [19,20] indicated that alder (*Alnus glutinosa*) trees and wild tobacco (*Nicotiana attenuata*) plants experienced less natural damage by herbivores when grown in close proximity to experimentally clipped neighbors, which were other alder trees in the first case and sagebrush (*Artemisia tridentata*) plants in the second case. In addition, barley (*Hordeum vulgare*) plants became less attractive to aphids after exposure to air from various thistle (*Cirsium*) species [21], an effect that can protect barley under field conditions [22]. Interestingly, barley responds to VOCs released from intact plants, which can be thistles or other barley cultivars [21,23]. These experiments demonstrated that airborne signals can affect the resistance of the receiver in the field. However, because they relied on air moving among plants, they left open the question as to which chemical cues were causing the observed effects.

Even the ecological relevance of these reports was still questioned, because the effects diminished as the distance between plants increased; either monotonically in the alder system [19] or beyond a threshold of 10–15 cm for tobacco and sagebrush [24]. However, sagebrush can affect resistance expression in plants growing at distances of up to 60 cm, which is within the range of sagebrush neighbors in nature [10]. Lima bean (*Phaseolus lunatus*) has also become a model system for studying plant communication [5,25]. In this case, the twining growth of wild beans places individuals in close proximity under natural growing conditions [4].

Resistance to herbivores and pathogens induced by airborne signals

The number of reports on plant–plant communication is now increasing rapidly (Table 1). Whereas the initial publications from 1983 were followed by only three more over

the following ten years, near to 50 empirical and review articles have been published on this topic since 2005 (numbers of publications found in the ISI Web of Science® in a search for the terms ‘plant–plant communication’, ‘plant–plant signaling’, ‘plant–plant signalling’ and ‘plant communication’ as well as for reports on the expression of defense genes or traits in plants exposed to plant-derived VOCs). That air coming from induced plants (and purportedly the VOCs contained in this air) trigger phenotypic resistance and/or the expression of resistance-related genes in intact plants has now been reported for the above mentioned species and also for *Arabidopsis thaliana* [26], corn (*Zea mays*) [18,27], cotton (*Gossypium hirsutum*) [15], broad bean (*Vicia faba*) [28] and tomato (*Lycopersicon esculentum* [14]; new name: *Solanum lycopersicum*; see URL: http://sgn.cornell.edu/about/solanum_nomenclature.pl).

Interestingly, although model species have received increasing interest over the past few years, most studies on plant communication have been conducted in an ecological context and focused on the anti-herbivore defense of wild, non-model plants (Table 1). As a consequence, less is known about volatile-mediated signaling in model plants and on induction of resistance to pathogens by airborne signals. Many questions concerning the underlying molecular mechanisms, particularly of the perception of volatile signals by intact plants, remain unanswered. In the context of pathogen resistance, it has been reported that air from virus-infected tobacco elicited systemic acquired resistance (SAR) to infection in intact plants and that this effect was probably caused by high concentrations of the volatile hormone, methyl salicylate [16]. The central role of methyl salicylate in tobacco SAR signaling [29] and the observation that VOCs can induce resistance of *Arabidopsis* to fungi [30] make it likely that plant communication also affects pathogen resistance (Figure 1).

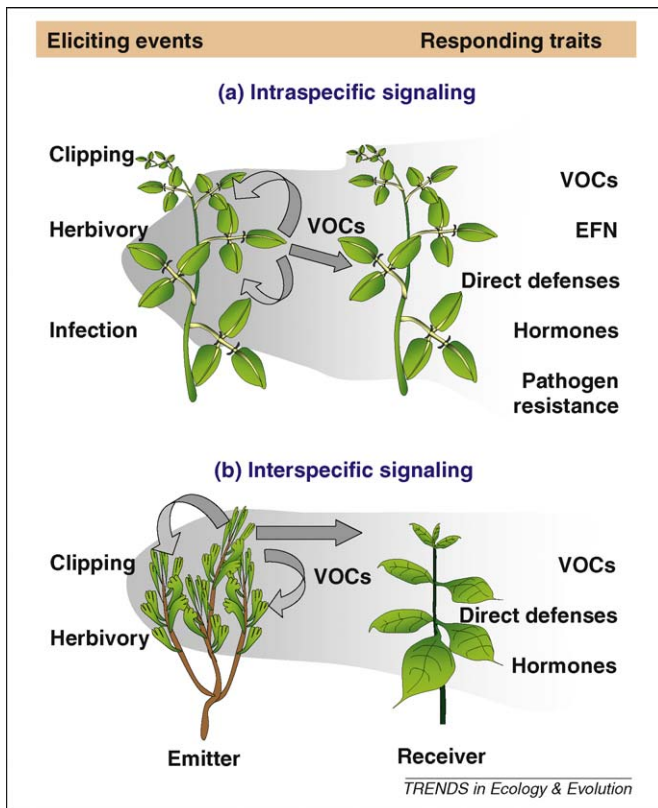


Figure 1. Factors causing and traits affected by volatile-mediated signaling among plants. VOCs released from damaged leaves (arrows) reach other leaves of the same plant and neighboring plants and can therefore mediate both within-plant signaling and plant-plant signaling. Intraspecific signaling (a) has been reported for black alder [19], corn [18,27], cotton [15], lima bean [5], poplar and sugar maple [2], sagebrush [10], Sitka willow [1] and tobacco [16]. VOCs that are released from plants in response to manual clipping, natural herbivore damage or pathogen infection affect direct defenses against herbivores such as proteinase inhibitors and leaf phenolics, indirect defenses (e.g., the release of VOCs and the secretion of extrafloral nectar), the production of the signaling hormones (SA and JA) and plant pathogen resistance. Interspecific signaling (b) has so far been reported in the case of tobacco [20] and tomato [14] plants exposed to damaged sagebrush and for induced resistance against aphids in barley exposed to *Cirsium* plants [21].

Fitness benefits

In spite of the comparably high number of ecological studies, there have been few attempts to estimate the fitness consequences of plant-plant signaling, probably because methods were missing to enable the controlled exchange of air (or purified VOCs) among plants under field conditions. However, responding to volatile cues increased components of receiver fitness in those systems where this has been measured. For example, lima bean tendrils exposed to herbivore-induced volatiles lost less leaf area to herbivores and produced more leaves and inflorescences than did controls in field experiments [4,5]. Wild tobacco plants whose defenses were induced by VOCs released from a damaged sagebrush neighbor produced as many or more flowers and seeds as non-induced controls in experiments that were repeated every year for five years [6].

Consequences of plant communication: emitters exploited by receivers?

In the above cited examples of volatile plant communication, the receiver altered its level of resistance, whereas benefits for the emitter have been reported only in the case

of VOC-mediated allelopathy [31–33]. Parasitic plants [34] and herbivorous insects [35–44] can use VOCs to locate their hosts, thereby exerting purportedly high ecological costs of VOC release on the emitter. In short, the perception of airborne cues usually benefits the receiver, whereas their release incurs a metabolic cost to the emitter [45] and might cause even higher costs when herbivores or parasitic plants use these VOCs as host-finding cues [34–44]. Moreover, improving the resistance of the neighbor might shift the competitive balance between emitter and receiver towards a disadvantage for the emitter, which is already damaged but probably helps its neighbor to avoid attack successfully.

Intriguingly, no study has yet demonstrated that resistance induction in intact neighbors can benefit the VOC-emitting plant. Should the phenomenon therefore be termed ‘eavesdropping’ rather than ‘communication’? Eavesdropping plants gain information about their risk of herbivory and adjust their defenses accordingly, enabling them to invest fewer costly resources when defenses are not needed, to gear up defenses in environments with high risk of attack, and possibly to tailor their defenses to the specific attacker. But why should plants emit the signals that are used by eavesdroppers?

In the following sections we discuss four non-exclusive explanations for the evolutionary onset and stability of VOC-mediated plant-plant signaling, which comprise: (i) VOC-mediated direct defense against biotic and abiotic stress; (ii) the role of VOCs in within-plant signaling; (iii) synergistic effects among VOCs and other types of induced resistance; and (iv) theories that are based on ideas of kin selection or group selection.

VOC-mediated defense of the emitter

Early explanations of the release of VOCs from herbivore-damaged plants focused on the direct defensive functions of these compounds [46]: herbivore-induced VOCs can repel herbivores [39,47–50], have antimicrobial effects [51–54] or protect plants from abiotic stress [55,56]. It was therefore suggested that VOCs serve mainly physiological plant functions and that their release is an unavoidable consequence of their physicochemical properties (high volatility and easy transmission through membranes) rather than an adaptive trait [46]. In this scenario, the attraction of predators, such as parasitic wasps and carnivorous mites [57–61], and the perception of VOCs by neighboring plants would be secondary effects that, independently of any effects on the fitness of the emitter, evolved as a consequence of the presence of VOCs in the atmosphere. These secondary effects would not even necessarily pose any significant evolutionary pressure on the production - and release - of VOCs.

VOCs in within-plant signaling

The direct protective effects of VOCs discussed above can explain why VOCs are emitted from attacked plants. But how did plants evolve the genetic and biochemical mechanisms that are required for their perception? Recent empirical findings [4,9–11] provide an attractive physiological explanation of why plants have evolved the capacity to both emit and to perceive VOCs: VOCs can play an

important role as internal plant signals. Studies of sagebrush, lima bean, poplar and blueberry (*Vaccinium corymbosum*) have demonstrated that VOCs released from the damaged parts of a plant induce resistance in undamaged organs of the same individual [4,9–11]. As proposed earlier [62,63], within-plant signaling by VOCs is faster than vascular signaling and independent of plant anatomy. These traits make VOCs capable of reaching non-orthostichous leaves (that is, leaves lacking direct vascular connections) and leaves that are located close in space to the attacked leaves but attached to different branches. Second, green-leaf volatiles are released immediately after cell damage and therefore provide rapid, reliable and highly mobile signals of the ‘damaged self’, making them an excellent cue to prepare systemic organs for future attack [64].

Third, lower doses of VOCs usually prime rather than fully induce resistance responses [4,9,18,25,27,65]: primed tissues do not show phenotypic changes in their resistance level but they respond faster and more strongly once attacked [66,67]. For example, lima bean shoots responded to the same intensity of mechanical damage with a stronger induction of extrafloral nectar (EFN) secretion when they had been exposed previously to VOCs that indicated the presence of damaged neighbors [25]. Similarly, resistance-related genes in maize were expressed faster after caterpillar feeding when the plants previously had been exposed to VOCs released from caterpillar-infested plants [27]. This mechanism adds a significant level of flexibility to airborne signaling within and among plants that had not been considered in earlier theoretical considerations. Any full induction of systemic resistance by local damage comes with the risk of investing in a defense that is not needed because local responses might successfully hinder the spread of the original attacker or because herbivores eventually leave the attacked plant for other reasons. Therefore, self-priming by VOCs (as reported for lima bean, poplar and blueberry [4,9,11]) allows a plant to prepare its systemic, not yet attacked organs for the upcoming attack without requiring high investment in a defense that is probably never needed [67].

Priming can also explain the positive fitness effects observed when wild tobacco plants were induced by manually damaging a sagebrush neighbor [6]. At first glance, this is a surprising result because the experimental induction signal provided misinformation about a high risk of herbivory. However, it is likely that the plants were primed rather than fully induced by the volatiles [65] and therefore only responded with full resistance expression when under attack from natural herbivores. Plants, thus, need to be able to emit and to perceive VOCs to achieve the full phenotypic plasticity that is required for a complete and efficient systemic resistance response; therefore, it is likely that signaling among plants evolved from within-plant signaling [67].

Synergistic effects among defense traits

VOCs can induce numerous responses, such as the expression of direct defenses [9,14,15,18,21,27] and the secretion of extrafloral nectar [4,5,25,68,69]. EFN attracts and enhances the survival of ants, parasitic wasps and other

predators because it contributes to their carbohydrate and amino acid uptake. Because many of these predators are attracted by VOCs [70–72], synergistic interactions among VOCs and other defenses might significantly enhance their efficacy [73]. Similarly, parasitism does not kill the parasitized herbivores immediately and as such does not provide an effective plant defense on its own, particularly when parasitism causes the host caterpillar to increase its feeding rate [74]. Moreover, many parasites can only attack first- or second-instar larvae, easily enabling herbivore larvae to ‘escape’ from being parasitized. Reports on beneficial effects of the parasitism of caterpillars are, therefore, scarce and restricted to laboratory systems [75,76]. However, if VOCs induce direct defenses in addition to attracting parasites, their negative effects on herbivore development can slow down caterpillar growth and therefore increase both the exposure of caterpillars to parasites and the effects of parasitism [41].

Kin selection

Models that use ideas based on group selection theory to explain information transfer among plants [77] stress the importance of successful resistance expression in neighboring plants. Assuming that these functions of VOCs are dose dependent, any induction of VOC release could help to increase their overall efficacy at the level of the plant population [77]. This is particularly the case when we consider that high phenotypic plasticity, and the resulting heterogeneous resistance expression at the population level, poses additional problems for the evolution of counter-adaptations by herbivores and pathogens [78].

Such systems would, however, be easily invaded by cheaters [79]. Later theoretical models adopted kin selection theory [80] and pointed to the fact that altruism is more stable in populations with limited dispersal, where the neighbors of a plant are likely to be closely related because a high proportion of them are composed of its direct offspring. In this situation, helping neighbors could increase the inclusive fitness of an individual via positive effects on the survival of its offspring [81,82]. Even with efficient pollination and dispersal mechanisms, most plants exchange pollen with their close neighbors and most seeds germinate close to the mother: therefore, plants might fulfill these theoretical requirements. In summary, airborne signaling can partly be explained by models of altruism that involve positive effects on inclusive fitness [79].

If plant defense operates via tritrophic interactions, predators need to be drawn to the damaged individual. Non-infested neighbors that attract predators could reduce the number of predators that recruit to the infested plant; this effect would spatially ‘dilute’ the defensive function rather than increasing its efficacy. Furthermore, emissions of VOCs from non-infested plants [15,18,83] that signal the presence of herbivores to predators would reduce signal reliability, thereby compromising the future responses of the predator to the signal in question. To avoid these problems, VOCs would have to be emitted in significantly higher amounts from the originally infested as compared with the secondarily induced tissues to provide predators with reliable, concentration-based guidance to the indu-

cing herbivore. A concerted repellence of herbivores seems to cause fewer problems in this respect, because it benefits all plants involved. However, both scenarios discussed here apply only to VOC release that is induced by VOCs and not to cases in which VOCs induce other defense traits, such as extrafloral nectar [4,5,25,68,69] or direct defenses [9,14,15,18,21,27]. Finally, although recent results suggest that sagebrush communicates more effectively with genetically identical ramets than with non-self ramets [84], kin selection theory fails to explain airborne signaling among unrelated plants [20–22].

Conclusions and outlook

When we tried to use empirical data to test the theoretical considerations discussed above, an imbalance became obvious: empirical research has focused on the effects of receiving volatiles, whereas theoreticians have focused on explaining airborne plant–plant communication from the point of view of the emitter. Moreover, all the forces mentioned above might have favored the development of the capacities required to synthesize and emit VOCs. By contrast, the discovery of within-plant signaling by VOCs provides an attractive explanation for the evolutionary origin of the physiological machinery that is needed to perceive volatile signals and to translate this information into purportedly adaptive responses. Finally, although the specificity of the perception [26,69,85] and of the elicited gene responses [17,18,27,86] has been described, there is still a lack of a molecular understanding of the perception mechanism.

In summary, there are theories at hand that could explain the evolution of emitting airborne signals but there is a lack of empirical data to test them. It is known empirically that plants can perceive VOCs but there are no theoretical models to understand the evolutionary origin of this capacity, neither is it known how volatiles are perceived and translated into signals.

Even after accepting plant–plant signaling via airborne cues as a physiological possibility, many researchers have doubted its ecological relevance [12,13,46], given that positive reports were restricted to very short distances. Evolutionary models [79] discussed high ‘viscosity’ in plant populations, making it likely that the ‘warned’ neighbor is a close relative, but data from at least two systems [20,21] demonstrate that being related is not a prerequisite for communication. However, VOC-mediated signaling also occurs among tissues and organs of the same plant. This process does not stop at the surface of the plant, but also affects other shoots of the same plant and neighboring, physiologically independent plants. Discovering the role of airborne signals in systemic within-plant signaling opens new evolutionary explanations for plant–plant signaling. Clonal dispersal and other mechanisms of population viscosity can facilitate the evolution of altruism because they increase the probability of interacting with closely related neighbors [82]. Kin selection-based theories [79,81] can therefore explain communication, particularly in clonal plant species. However, these ideas can also be applied to non-clonal plants with complex anatomies: the branched structure of lianae, shrubs and trees ensures that most organs that are exposed to VOCs being released from a

damaged leaf will usually form part of the same individual. The ‘shortcoming’ that VOC-mediated signaling functions over comparably short distances might rather represent a benefit, because it reduces the probability of eavesdropping by non-related neighbors, perhaps below an evolutionarily relevant threshold.

Whether signaling among different plants via airborne cues is referred to as ‘communication’ depends on the detailed definition applied. More importantly, however, there is a lack of empirical data on the effects of this phenomenon on the fitness of the emitter. Future studies aimed at understanding ‘plant communication’ will have to consider the consequences of interplant signaling on both the emitter and the receiver and will have to separate the consequences of VOC-mediated effects on neighboring plants from the multiple functions of VOCs in within-plant signaling and in other interactions.

Acknowledgements

We are grateful to three anonymous referees for many constructive comments on earlier versions of this manuscript. MH acknowledges financial support by the Deutsche Forschungsgemeinschaft (DFG grant He3169/4–2) and CONACyT de México.

References

- Rhoades, D.F. (1983) Responses of alder and willow to attack by tent caterpillars and webworms: evidence for pheromonal sensitivity of willows. In *Plant Resistance to Insects* (Hedin, P.A., ed.), pp. 55–68, American Chemical Society
- Baldwin, I.T. and Schultz, J.C. (1983) Rapid changes in tree leaf chemistry induced by damage: evidence for communication between plants. *Science* 221, 277–279
- Karban, R. (2008) Plant behaviour and communication. *Ecol. Lett.* 11, 727–739
- Heil, M. and Silva Bueno, J.C. (2007) Within-plant signaling by volatiles leads to induction and priming of an indirect plant defense in nature. *Proc. Natl. Acad. Sci. U. S. A.* 104, 5467–5472
- Kost, C. and Heil, M. (2006) Herbivore-induced plant volatiles induce an indirect defence in neighbouring plants. *J. Ecol.* 94, 619–628
- Karban, R. and Maron, J. (2002) The fitness consequences of interspecific eavesdropping between plants. *Ecology* 83, 1209–1213
- Kessler, A. and Baldwin, I.T. (2002) Plant responses to insect herbivory: the emerging molecular analysis. *Annu. Rev. Plant Biol.* 53, 299–328
- Durrant, W.E. and Dong, X. (2004) Systemic acquired resistance. *Annu. Rev. Phytopathol.* 42, 185–209
- Frost, C. *et al.* (2007) Within-plant signalling by volatiles overcomes vascular constraints on systemic signalling and primes responses against herbivores. *Ecol. Lett.* 10, 490–498
- Karban, R. *et al.* (2006) Damage-induced resistance in sagebrush: volatiles are key to intra- and interplant communication. *Ecology* 87, 922–930
- Rodríguez-Saona, C.R. *et al.* (2009) Herbivore-induced volatiles in the perennial shrub, *Vaccinium corymbosum*, and their role in inter-branch signaling. *J. Chem. Ecol.* 35, 163–175
- Fowler, S.V. and Lawton, J.H. (1985) Rapidly induced defenses and talking trees: the devil’s advocate position. *Am. Nat.* 126, 181–195
- Dicke, M. and Bruin, J. (2001) Chemical information transfer between plants: back to the future. *Biochem. Syst. Ecol.* 29, 981–994
- Farmer, E.E. and Ryan, C.A. (1990) Interplant communication: airborne methyl jasmonate induces synthesis of proteinase inhibitors in plant leaves. *Proc. Natl. Acad. Sci. U. S. A.* 87, 7713–7716
- Bruin, J. *et al.* (1992) Plants are better protected against spider-mites after exposure to volatiles from infested conspecifics. *Experientia* 48, 525–529
- Shulaev, V. *et al.* (1997) Airborne signalling by methyl salicylate in plant pathogen resistance. *Nature* 385, 718–721
- Arimura, G-I. *et al.* (2000) Herbivory-induced volatiles elicit defence genes in lima bean leaves. *Nature* 406, 512–515

- 18 Engelberth, J. *et al.* (2004) Airborne signals prime plants against insect herbivore attack. *Proc. Natl. Acad. Sci. U. S. A.* 101, 1781–1785
- 19 Dolch, R. and Tschardtke, T. (2000) Defoliation of alders (*Alnus glutinosa*) affects herbivory by leaf beetles on undamaged neighbours. *Oecologia* 125, 504–511
- 20 Karban, R. *et al.* (2000) Communication between plants: induced resistance in wild tobacco plants following clipping of neighboring sagebrush. *Oecologia* 125, 66–71
- 21 Glinwood, R. *et al.* (2004) Barley exposed to aerial allelopathy from thistles (*Cirsium* spp.) becomes less acceptable to aphids. *Ecol. Entomol.* 29, 188–195
- 22 Ninkovic, V. *et al.* (2009) Weed–barley interactions affect plant acceptance by aphids in laboratory and field experiments. *Entomol. Exp. Appl.* 133, 38–45
- 23 Glinwood, R. *et al.* (2009) Airborne interactions between undamaged plants of different cultivars affect insect herbivores and natural enemies. *Arthropod-Plant Interact.* publ. online doi:10.1007/s11829-009-9072-9
- 24 Karban, R. *et al.* (2003) Herbivore damage to sagebrush induces resistance in wild tobacco: evidence for eavesdropping between plants. *Oikos* 100, 325–332
- 25 Heil, M. and Kost, C. (2006) Priming of indirect defences. *Ecol. Lett.* 9, 813–817
- 26 Godard, K.A. *et al.* (2008) Monoterpene-induced molecular responses in *Arabidopsis thaliana*. *Phytochemistry* 69, 1838–1849
- 27 Ton, J. *et al.* (2007) Priming by airborne signals boosts direct and indirect resistance in maize. *Plant J.* 49, 16–26
- 28 Birkett, M.A. *et al.* (2000) New roles for cis-jasmone as an insect semiochemical and in plant defense. *Proc. Natl. Acad. Sci. U. S. A.* 97, 9329–9334
- 29 Park, S.W. *et al.* (2007) Methyl salicylate is a critical mobile signal for plant systemic acquired resistance. *Science* 318, 113–116
- 30 Kishimoto, K. *et al.* (2005) Volatile C6-aldehydes and allo-ocimene activate defense genes and induce resistance against *Botrytis cinerea* in *Arabidopsis thaliana*. *Plant Cell Physiol.* 46, 1093–1102
- 31 Ninkovic, V. (2003) Volatile communication between barley plants affects biomass allocation. *J. Exp. Bot.* 54, 1931–1939
- 32 Karban, R. (2007) Experimental clipping of sagebrush inhibits seed germination of neighbours. *Ecol. Lett.* 10, 791–797
- 33 Barney, J.N. *et al.* (2009) Biogenic volatile organic compounds from an invasive species: impacts on plant–plant interactions. *Plant Ecol.* 203, 195–205
- 34 Runyon, J.B. *et al.* (2006) Volatile chemical cues guide host location and host selection by parasitic plants. *Science* 313, 1964–1967
- 35 Frati, F. *et al.* (2008) Role of the plant-conspecific complex in host location and intra-specific communication of *Lygus rugulipennis*. *Physiol. Entomol.* 33, 129–137
- 36 Frati, F. *et al.* (2009) *Vicia faba*–*Lygus rugulipennis* interactions: induced plant volatiles and sex pheromone enhancement. *J. Chem. Ecol.* 35, 201–208
- 37 Brilli, F. *et al.* (2009) Constitutive and herbivore-induced monoterpenes emitted by *Populus x euroamericana* leaves are key volatiles that orient *Chrysomela populi* beetles. *Plant Cell Environ.* 32, 542–552
- 38 Garcia-Robledo, C. and Horvitz, C.C. (2009) Host plant scents attract rolled-leaf beetles to Neotropical gingers in a Central American tropical rain forest. *Entomol. Exp. Appl.* 131, 115–120
- 39 Heil, M. (2004) Direct defense or ecological costs?? Responses of herbivorous beetles to volatiles released by wild Lima bean (*Phaseolus lunatus*). *J. Chem. Ecol.* 30, 1289–1295
- 40 Jordan, M.D. *et al.* (2009) Odorant receptors from the light brown Apple Moth (*Epiphyas postvittana*) recognize important volatile compounds produced by plants. *Chem. Senses* 34, 383–394
- 41 Dicke, M. and van Loon, J.J.A. (2000) Multitrophic effects of herbivore-induced plant volatiles in an evolutionary context. *Entomol. Exp. Appl.* 97, 237–249
- 42 Bolter, C.J. *et al.* (1997) Attraction of Colorado potato beetle to herbivore-damaged plants during herbivory and after its termination. *J. Chem. Ecol.* 23, 1003–1023
- 43 Kalberer, N.M. *et al.* (2001) Attraction of a leaf beetle (*Oreina cacaliae*) to damaged host plants. *J. Chem. Ecol.* 27, 647–661
- 44 Mooney, A.C. *et al.* (2009) Neonate silkworm (*Bombyx mori*) larvae are attracted to mulberry (*Morus alba*) leaves with conspecific feeding damage. *J. Chem. Ecol.* 35, 552–559
- 45 Hoballah, M.E. *et al.* (2004) Costs of induced volatile production in maize. *Oikos* 105, 168–180
- 46 Peñuelas, J. and Llusià, J. (2004) Plant VOC emissions: making use of the unavoidable. *Trends Ecol. Evol.* 19, 402–404
- 47 de Moraes, C.M. *et al.* (2001) Caterpillar-induced nocturnal plant volatiles repel conspecific females. *Nature* 410, 577–580
- 48 Kessler, A. and Baldwin, I.T. (2001) Defensive function of herbivore-induced plant volatile emissions in nature. *Science* 291, 2141–2144
- 49 Bruinsma, M. *et al.* (2008) Differential effects of jasmonic acid treatment of *Brassica nigra* on the attraction of pollinators, parasitoids, and butterflies. *Entomol. Exp. Appl.* 128, 109–116
- 50 Bernasconi, M.L. *et al.* (1998) Herbivore-induced emissions of maize volatiles repel the corn leaf aphid, *Rhagoletis maidis*. *Entomol. Exp. Appl.* 87, 133–142
- 51 Dilantha Fernando, W.G. *et al.* (2005) Identification and use of potential bacterial organic antifungal volatiles in biocontrol. *Soil Biol. Biochem.* 37, 955–964
- 52 Nakamura, S. and Hatanaka, A. (2002) Green-leaf-derived C6-aroama compounds with potent antibacterial action that act on both gram-negative and gram-positive bacteria. *J. Agricult. Food Chem.* 50, 7639–7644
- 53 Matsui, K. (2006) Green leaf volatiles: hydroperoxide lyase pathway of oxylipin metabolism. *Curr. Opin. Plant Biol.* 9, 274–280
- 54 Shiojiri, K. *et al.* (2006) Changing green leaf volatile biosynthesis in plants: An approach for improving plant resistance against both herbivores and pathogens. *Proc. Natl. Acad. Sci. U. S. A.* 103, 16672–16676
- 55 Behnke, K. *et al.* (2007) Transgenic, non-isoprene emitting poplars don't like it hot. *Plant J.* 51, 485–499
- 56 Loreto, F. and Velikova, V. (2001) Isoprene produced by leaves protects the photosynthetic apparatus against ozone damage, quenches ozone products, and reduces lipid peroxidation of cellular membranes. *Plant Physiol.* 127, 1781–1787
- 57 Dicke, M. and Sabelis, M.W. (1988) How plants obtain predatory mites as bodyguards. *Netherl. J. Zool.* 38, 148–165
- 58 Turlings, T.C.J. *et al.* (1990) Exploitation of herbivore-induced plant odors by host-seeking parasitic wasps. *Science* 250, 1251–1253
- 59 Tumlinson, J.H. *et al.* (1999) Plant production of volatile semiochemicals in response to insect-derived elicitors. In *Insect-Plant Interactions and Induced Plant Defence* (Chadwick, D.J. and Goode, J.A., eds), pp. 95–109, Wiley
- 60 de Moraes, C.M. *et al.* (1998) Herbivore-infested plants selectively attract parasitoids. *Nature* 393, 570–573
- 61 Bruinsma, M. *et al.* (2009) Jasmonic acid-induced volatiles of *Brassica oleracea* attract parasitoids: effects of time and dose, and comparison with induction by herbivores. *J. Exp. Bot.* 60, 2575–2587
- 62 Farmer, E.E. (2001) Surface-to-air signals. *Nature* 411, 854–856
- 63 Orians, C. (2005) Herbivores, vascular pathways, and systemic induction: facts and artifacts. *J. Chem. Ecol.* 31, 2231–2242
- 64 Heil, M. (2009) Damaged-self recognition in plant herbivore defence. *Trends Plant Sci.* 14, 356–363
- 65 Kessler, A. *et al.* (2006) Priming of plant defense responses in nature by airborne signaling between *Artemisia tridentata* and *Nicotiana attenuata*. *Oecologia* 148, 280–292
- 66 Conrath, U. *et al.* (2006) Priming: Getting ready for battle. *Mol. Plant Microbe Interact.* 19, 106–1071
- 67 Heil, M. and Ton, J. (2008) Long-distance signalling in plant defence. *Trends Plant Sci.* 13, 264–272
- 68 Choh, Y. *et al.* (2006) Induced production of extrafloral nectar in intact lima bean plants in response to volatiles from spider mite-infested conspecific plants as a possible indirect defense against spider mites. *Oecologia* 147, 455–460
- 69 Heil, M. *et al.* (2008) Defence-inducing volatiles: in search for the active motif. *J. Chem. Ecol.* 34, 601–604
- 70 Röse, U.S.R. *et al.* (2006) Extrafloral nectar from cotton (*Gossypium hirsutum*) as a food source for parasitic wasps. *Funct. Ecol.* 20, 67–74
- 71 Lee, J.C. and Heimpel, G.E. (2007) Sugar feeding reduces short-term activity of a parasitoid wasp. *Physiol. Entomol.* 32, 99–103
- 72 Limburg, D.D. and Rosenheim, J.A. (2001) Extrafloral nectar consumption and its influence on survival and development of an

- omnivorous predator, larval *Chrysoperla plorabunda* (Neuroptera: Chrysopidae). *Environ. Entomol.* 30, 595–604
- 73 Heil, M. (2008) Indirect defence via tritrophic interactions. *New Phytol.* 178, 41–61
- 74 Hoballah, M.E. *et al.* (2004) Occurrence and direct control potential of parasitoids and predators of the fall armyworm (Lepidoptera: Noctuidae) on maize in the subtropical lowlands of Mexico. *Agricult. Forest Entomol.* 6, 83–88
- 75 Fritzsche Hoballah, M.E. and Turlings, T.C.J. (2001) Experimental evidence that plants under caterpillar attack may benefit from attracting parasitoids. *Evol. Ecol. Res.* 3, 553–565
- 76 van Loon, J.J.A. *et al.* (2000) Parasitoid-plant mutualism: parasitoid attack of herbivore resistance increases plant reproduction. *Entomol. Exp. Appl.* 97, 219–227
- 77 Bruin, J. and Dicke, M. (2001) Chemical information transfer between wounded and unwounded plants: backing up the future. *Biochem. Syst. Ecol.* 29, 1103–1113
- 78 Agrawal, A.A. (2001) Phenotypic plasticity in the interactions and evolution of species. *Science* 294, 321–326
- 79 Kobayashi, Y. and Yamamura, N. (2007) Evolution of signal emission by uninfested plants to help nearby infested relatives. *Evol. Ecol.* 21, 281–294
- 80 Hamilton, W.D. (1964) The genetical evolution of social behaviour I and II. *J. Theor. Biol.* 7, 1–16 and 17–52
- 81 El Mouden, C. and Gardner, A. (2008) Nice natives and mean migrants: the evolution of dispersal-dependent social behaviour in viscous populations. *J. Evol. Biol.* 21, 1480–1491
- 82 Gardner, A. and West, S.A. (2006) Demography, altruism, and the benefits of budding. *J. Evol. Biol.* 19, 1707–1716
- 83 Ruther, J. and Fürstenau, B. (2005) Emission of herbivore-induced volatiles in absence of a herbivore - Response of *Zea mays* to green leaf volatiles and terpenoids. *Z. Naturforsch. C Biosci.* 60, 743–756
- 84 Karban, R. and Shiojiri, K. (2009) Self-recognition affects plant communication and defense. *Ecol. Lett.* 12, 502–506
- 85 Almeras, E. *et al.* (2003) Reactive electrophile species activate defense gene expression in *Arabidopsis*. *Plant J.* 34, 202–216
- 86 Engelberth, J. *et al.* (2007) Insect elicitors and exposure to green leafy volatiles differentially upregulate major octadecanoids and transcripts of 12-oxo phytodieneic acid reductases in *Zea mays*. *Mol. Plant Microbe Interact.* 20, 707–716
- 87 Kautz, S. *et al.* (2009) How to prevent cheating: a digestive specialization ties mutualistic plant-ants to their ant-plant partners. *Evolution* 63, 839–853
- 88 Loughrin, J.H. *et al.* (1994) Diurnal cycle of emission of induced volatile terpenoids by herbivore-injured cotton plants. *Proc. Natl. Acad. Sci. U. S. A.* 91, 11836–11840
- 89 Karban, R. *et al.* (2004) The specificity of eavesdropping on sagebrush by other plants. *Ecology* 85, 1846–1852