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Do plants tap SOS signals from their infested neighbours?

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Ecologists have not been able to show unambiguous evidence for the involvement of plant-to-plant signal transfer in the defence strategies of plants. However, phytopathologists and plant physiologists recently demonstrated that resistance in undamaged plants can be elicited by volatiles of plant origin. Now that empirical evidence is accumulating, there is every reason to ask why plants use the available information on the infestation status of their neighbours and to assess the fitness advantages associated with the tuning of their defence. The debate on the ecological and evolutionary significance of interplant communication needs to be revived.

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Plant individuals can be interconnected in many ways, mainly differing in the nature of the medium. One obvious way is direct contact between the root systems, by means of root grafts or haustoria^{1,2}. Alternatively, physical contact is achieved via mediating organisms, such as mycorrhizal fungi^{3,4}. In fact, associations between plants and mycorrhizal fungi are so widespread that there is much opportunity for plants to become interconnected with other plants in the community via hyphal bridges. Physical contact is not limited to conspecific plants; plants of different species also can be linked. In both situations, actual transport of substances – mineral nutrients, carbohydrates – has been shown^{4,5}. Plant-to-plant contact need not be via organismal connections; water and air can also transfer chemicals from one plant to another. Well-known examples stem from research on allelopathic interactions, where one plant can influence a neighbouring plant via water-dissolved sprout leachates or root exudates, or via volatile substances such as ethylene⁶. Ethylene is widely known to

induce a suite of physiological changes both within and between plants⁷. In summary, plant-to-plant transfer of chemicals exists beyond doubt.

Airborne information transfer between plants: ecological studies

Transfer of chemicals between plants was commonly studied in the context of nutrition (apparent mutualism) or competition (allelopathy). Whether such transfer also involves volatiles from infested plants that mediate defensive responses in uninfested plants has been the subject of considerable debate in the ecological literature. Rhoades^{8,9} carried out experiments with young trees [red alder (*Alnus rubra*) and Sitka willow (*Salix sitchensis*)] and their insect herbivores [webworms (*Hyphantria cunea*) and tent caterpillars (*Malacosoma californicum pluviale*)], and found lower performance of the herbivores on trees exposed to volatiles from conspecific infested trees. However, Fowler and Lawton¹⁰ emphasized the possibility of airborne transfer of caterpillar pathogens as an alternative explanation for these results. Under more controlled conditions, Baldwin and Schultz¹¹ did similar experiments with potted tree seedlings [poplar (*Populus × euroamericana*) and sugar maple (*Acer saccharum*)] that were or were not artificially damaged. They found elevated levels of phenolic compounds in the seedlings exposed to volatiles from damaged conspecific seedlings, but did not go on to show that the induction of phenolics resulted in increased resistance. Their results, however, were criticized on statistical grounds (pseudoreplication)¹⁰.

Fowler and Lawton¹⁰ themselves performed a field experiment with artificially damaged birch saplings (*Betula pubescens pubescens*). Four weeks after manual defoliation, leaf damage from natural herbivory was assessed on untreated trees that were either nearby or further away from the damaged trees. No differences in leaf damage were found between the different treatments, and hence no evidence for plant-to-plant signal transfer. However, their experimental design seems very insensitive; for example, any short-term effect may easily have been overshadowed in the course of the month following the treatment. Haukioja and co-workers¹² carried out field experiments with another herbivore-tree system [autumnal moth caterpillar (*Epirrita autumnata*) and mountain birch (*B. pubescens tortuosa*)] and

found positive correlations between distance to the closest defoliated tree and various herbivore performance indices (e.g. growth, survival, egg production). Airborne pathogen spread was unlikely in their experiments as they used manual defoliation to damage the source tree, and their experiments did not suffer from statistical flaws. Thus, their results could be explained by airborne information transfer between plants, although passing of the triggering cue(s) via soil and roots cannot be ruled out.

Based upon a laboratory experiment, Lin and co-workers¹³ claimed to have found no evidence for (airborne) information transfer between plants: Mexican bean beetles (*Epilachna varivestis*) did not show a preference when offered a choice between leaves from uninjured soybean plants (*Glycine max*) that had been in a pot together with either a soybean plant that was injured by soybean loopers, or an uninjured control. But if the differently treated plants were all in the same room, as suggested in the report, these results might as well be interpreted as the consequence of airborne information transfer from infested to uninfested plants!

This overview of ecological studies shows that the evidence for mediation of a defensive response in uninfested plants via volatile signals from infested plants is ambiguous. As Fowler and Lawton¹⁰ rightly pointed out, it is encouraging to see similar phenomena in different plant species, but there is a need for better design and more adequate replication of the experiments. Rather than studying herbivore performance only, as in most of the above studies, it may be more fruitful to obtain direct mechanistic evidence for plant-to-plant signal transmission by focusing on the chemicals involved and on biochemical changes triggered in signal-receiving plants.

Airborne information transfer between plants: physiological studies

Direct chemical evidence for plant-to-plant signal transfer was recently published by a number of physiologists. Carefully controlled laboratory experiments revealed that resistance genes were activated in undamaged young tomato (*Lycopersicon esculentum*), alfalfa (*Medicago sativa*) and tobacco (*Nicotiana tabacum*) plants, after exposure to the vapour of methyl jasmonate^{14,15}. In all three species, methyl jasmonate, originating either from a synthetic solution or from sagebrush (*Artemisia tridentata tridentata*) twigs with undamaged leaves, was shown to induce the synthesis of proteinase inhibitors, the production of which is also enhanced by herbivore or

pathogen attack^{14,15}; proteinase inhibitors are thought to function as digestibility reducers and have been shown to lower insect attack¹⁶. These experiments unequivocally demonstrate the ability of unharmed plants to respond actively to volatile compounds that are of plant origin. Methyl jasmonate is a common plant compound, identified in members of at least nine families¹⁴. Although damaged plants generally produce higher levels of methyl jasmonate, the levels produced by undamaged sagebrush were shown to be high enough to elicit a defensive response in exposed plants. This finding raises the new puzzle as to why undamaged plants should take defensive measures when exposed to methyl jasmonate, produced by an undamaged plant.

Can defence responses in undamaged plants be triggered by a volatile signal that is exclusively derived from wounded plants? The experiment providing the closest answer to this question was done by Zeringue¹⁷. After exposure to a microbial-free blend of volatiles originating from cotton (*Gossypium hirsutum*) leaves infected with *Aspergillus flavus*, a significant increase of terpenoids (with insecticidal properties) was demonstrated in undamaged leaves. There was no increase when undamaged leaves were exposed to volatiles from either artificially damaged cotton leaves or fungus cultures on artificial media. Apparently, some infection-related change in the blend occurred, which caused a response in recipient leaves, but whether this response is effective against the fungi was not shown. The chemical compounds involved were not identified, so their plant origin still awaits final proof.

In a separate study, Zeringue¹⁸ offered purified plant volatiles (aldehydes) to (artificially damaged) cotton bolls and found an increase in antifungal phytoalexins, but in this study it is unclear how the volatiles relate to leaf damage caused by fungi. Similarly, Hildebrand and co-workers¹⁹ exposed tobacco (*N. tabacum*) leaf discs to synthetic plant volatiles, and found reduced aphid (*Myzus nicotianae*) fecundity on these leaf discs. The compounds tested are known to volatilize from crushed tomato (*L. esculentum*) leaves²⁰, but the relation of the volatiles to plant infestation is unclear. Moreover, actual chemical changes in exposed tobacco leaves remain to be shown. All these studies support the hypothesis that there is information transfer between damaged and undamaged plants.

Fuel for the 'talking tree' debate

While the evidence for information transfer may be compelling for plant physiologists, ecologists may still be skeptical because none of these studies provides a complete picture – in a more realistic set-

ting – of the chain of action and reaction, starting from the processes involved in damaging a plant, via the signals produced, to the response in the undamaged plant and its effect on potential damaging organisms. It is especially unsatisfying that the origin of the mediating volatiles is not clear from any of the chemical studies on information transfer between damaged and undamaged plants. So far, the causal relation between injury to a plant – by whatever organism – and the release of specified plant volatiles remained implicit.

In a number of quite different systems, however, such knowledge has accumulated: (1) bean (*Phaseolus vulgaris*) plants inoculated with phytopathogenic bacteria (*Pseudomonas syringae* pv. *phaseolicola*) start producing a number of volatile compounds that are not produced in healthy control plants²¹; (2) plants damaged by caterpillars (e.g. *Spodoptera exigua*) produce volatiles that attract parasitoids (e.g. *Cotesia marginiventris*), the natural enemies of the caterpillars^{22–24}; (3) plants damaged by spider mites (e.g. *Tetranychus urticae*) produce volatiles that attract predatory mites (e.g. *Phytoseiulus persimilis*)^{24–26}. All three systems seem good candidates for studying the influence of infestation-related plant volatiles on resistance in recipient undamaged plants (see also Box 1).

In one of these systems – the plant-mite system – it was shown that undamaged bean (*Phaseolus lunatus*) and cotton plants became attractive to predatory mites (*Phytoseiulus persimilis*) after exposure to volatiles from conspecific plants infested with *T. urticae*, and that the spider mites' oviposition rate was reduced on exposed plants^{25,27}. It remains to be shown which volatiles cause these effects, and how the exposed plants are involved. The latter question is important because the mediating volatiles may either induce an active physiological response in the receiving plant or simply adsorb to the plant's cuticle and volatilize again at a slower rate. The term *communication* could be reserved for mediation of active plant responses; the alternative, that is, passive mediation via adsorption, could be called *contamination*. Thus, although the origin of the chemicals is clear in the plant-mite system, it is still to be shown whether the mite responses are due to plant-to-plant communication or contamination.

Despite apparent shortcomings in all of the ecological and physiological studies, the chemical evidence demonstrates the possibility – if not the likelihood – of information transfer through the atmosphere from damaged to undamaged plants. This sheds new light on the experiments of Rhoades^{8,9} and Baldwin and Schultz¹¹, who were forced to stop any further investigation after the discussions led to com-

motion in the newspapers – now known as the 'talking tree' debate.

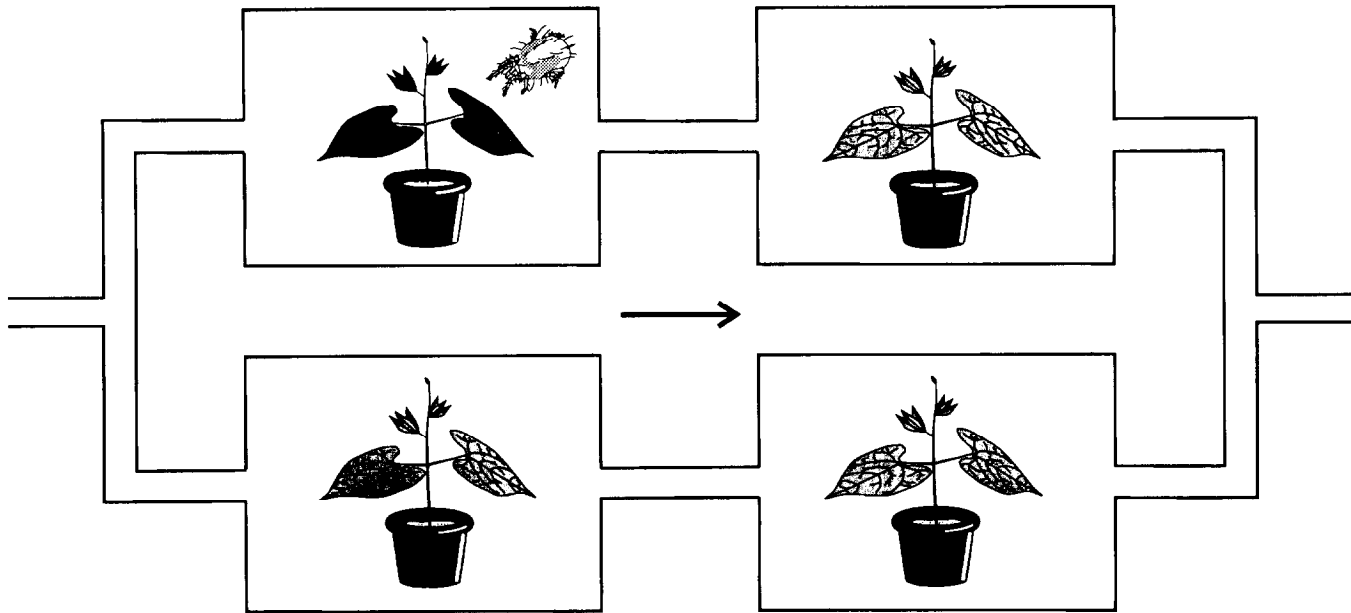
Damage-induced production of plant volatiles

Why would a damaged plant produce volatile substances to begin with? One can think of several, entirely different reasons. For example, the volatiles may arise simply as a result of biochemical processes following cell destruction. Or microorganisms, either symbiotic or wound-colonizing, may be the producers, rather than the plants. Regardless of their origin, however, the volatiles can affect the plant in various ways. First, volatile substances may have direct, adverse effects on the damaging agents themselves^{19,21,28} and on wound-colonizing microbes. Second, they may stimulate and coordinate systemic induction of resistance in single tree canopies, as suggested by Baldwin and Schultz¹¹. Although the direction of volatile signals is wind-dependent and cannot be controlled by a plant, this mode of signal transduction is fast and circumvents possible limitations of within-plant transduction channels²⁹. Third, plants may betray the presence of the damaging agent to its natural enemies (true predators and parasitoids)^{21–26}.

Each of these possible reasons for the existence of damage-induced volatiles may represent traits that are promoted by natural selection in the plant population. However, as volatiles can have multiple effects, it is possible that evolution of one trait influences evolution of the other. As an illustration of this point, consider the 'null' case where plants happen to produce volatiles after cell destruction. If some of the compounds have a negative effect on any wound-colonizing microorganism and/or herbivore, then natural selection benefits plant genotypes that produce more of these compounds. This may well lead to plant-specific responses to pathogen- or herbivore-specific damage. Given the presence of the volatile compounds, any predator using this information to find prey will gain a selective advantage, as it reduces the time spent in areas without prey. Hence, specific signalling may well lead to specific predator responses, and there is much room for coevolution to bring the information code to perfection. This cascade of evolutionary steps is just one of the many scenarios for the evolution of damage-induced production of volatiles.

Once airborne, plant chemicals represent information and the plant cannot control their use by other organisms. Indeed, it is not obvious, *a priori*, that an individual plant will gain an overall advantage by production of volatiles upon attack by a damaging agent. For example, if the volatiles lure parasitoids rather than (true) predators, the plant may not always

Box 1. A straightforward experimental design



This design allows for straightforward laboratory experiments, aimed at studying the influence of damage-related plant volatiles on resistance in recipient undamaged plants (a set-up like this was used in Refs 17 and 27). It consists of two parallel windtunnels, each consisting of two compartments in series. The small arrow in the centre indicates a unidirectional continuous air stream. Undamaged plants in the two downwind compartments are exposed to volatiles from either infested or uninfested plants; gauze and/or microbial traps in between two serial compartments will ensure that nothing but volatile chemicals reaches the downwind plants. Possible differences between the two (groups of) exposed, uninfested plants can then only be the result of exposure to damage-related volatiles. If desired, air can easily be purified before entering the apparatus, and it can be trapped for chemical analyses anywhere in the windtunnels. Moreover, in a design like this it is very easy to control variables such as wind speed, plant density, infestation level, etc. Plants can continuously be exposed to damage-related volatiles, or discontinuously, to simulate varying wind directions. After different durations of exposure, exposed plants can be taken from the set-up and used for further assays, such as behavioural experiments with natural enemies of herbivores in flight tunnels or olfactometers, or for chemical analyses. *Drawing by Arne Janssen.*

benefit because parasitoids do not always kill the host immediately; parasitization may even increase the overall per capita feeding damage by the host, so that an advantage to the plant may only accrue from the impact on next generation herbivores. The signal-emitting plant may incur even more adverse effects in that (1) it may attract an ineffective predator (which, on top of that, may outcompete the effective predators), (2) it may attract hyperpredators, and (3) it may attract other herbivores²⁶. Another possible disadvantage is that the alarm signals may warn unrelated neighbouring plants, which may then use the information to improve upon their competitive abilities, for example by allocating energy to direct defence against the damaging agents that are on their way³⁰. Overall risk-benefit assessments of damage-induced production of volatiles have not yet been carried out. Hence, one should be very wary of inferring adaptive significance of information transfer.

A functional view of interplant communication

Interplant communication provides an immediate advantage to both the sender and the receiver when the plants are sufficiently close kin. Independent of a sender's interest, a receiver plant does best

to take advantage of any volatile information that is around. It seems perfectly reasonable for plants to anticipate forthcoming damage after exposure to risk-associated signalling. Presence of the signal may inform the receiver of approaching doom and it allows the receiver to take timely measures. Herbivore-plant interactions may serve as an example (although much the same reasoning applies to plant pathogens). Air currents transferring the signals may (later) also carry the herbivores, and upon exposure the recipient plant may allocate energy either to direct defence, by increasing levels of toxins, digestion inhibitors, repellents, etc., or to indirect defence, by luring the natural enemies of the herbivore. As variation in wind direction implies periodic exposure to the alarm signal, it could pay the recipient plant to continue the defensive response beyond the periods of actual exposure, especially when the herbivores arrive by other means. If signal-exposed uninfested plants do take defensive action, then the sender could experience an extra benefit by being part of a group of plants with an alarmed defence system, thereby making the group as a whole less profitable for herbivores. In that case, herbivores will profit from foraging a distance away.

Prospects

If our tour from experiments to hypotheses on functions shows anything, then it is the need for ecologists to go back to the field and reassess the importance of plant-to-plant communication in more carefully designed field experiments. Physiologists have shown the possibilities for information transfer from damaged to undamaged plants, although they could have selected more realistic systems of interacting organisms. Now it is the ecologists' move. It may well be a difficult task to demonstrate significance of plant-to-plant communication, since effects may be small. However, small effects are not necessarily unimportant, as minute fitness gains can reach fixation in surprisingly few generations. Indeed, ecologists who set out to detect processes in the field by collecting data on average performance may well overlook phenomena that are vital to the individual organism in terms of its contribution to future generations.

If carefully controlled experiments provide no evidence in support of plant-to-plant communication, then one should not give up too soon. Such 'null' results^{10,13} should trigger new functional questions for much the same reasons as positive outcomes do. If plants are not found to take part in information transfer, then the

question should be whether they are incapable or whether they are 'unwilling' for good reasons.

The study of interplant communication deserves attention not only because of its intrinsic interest, but also because it is yet another field in which evolution in communication systems becomes manifest. There is much need for a theoretical understanding of the circumstances under which communication systems may evolve, as it may assist in their discovery and characterization^{31,32}.

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