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Chemical information transfer between plants: back to the future

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Abstract

Chemical information conveyance between organisms has been well established for a wide range of organisms including protozoa, invertebrates, vertebrates and plant-parasitic plants. During the past 20 years, various studies have addressed whether chemical information conveyance also occurs between damaged and undamaged plants and many interesting pieces of evidence have been presented. To date, this research field has been restricted to the question whether and how plants (in general) are involved in plant-to-plant communication. However, apart from mechanistic questions, evolutionary questions should be addressed asking why plants do (or do not) exploit their neighbour's information and whether their strategy is affected by e.g. environmental conditions or previous experience. Recent progress in the field of chemical information conveyance between damaged and undamaged plants warrants an intensified study of this exciting topic in chemical ecology. © 2001 Elsevier Science Ltd. All rights reserved.

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1. Introduction

All organisms are under selective pressure to maximize reproductive success. To exploit the prevailing environmental conditions to their full extent, organisms can take advantage of information. An important form of information consists of chemical cues. It has been well established that chemical information plays an essential role in the ecology of such diverse organisms as protozoa (Kuhlmann et al.,

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1999), crustaceans (Tollrian and Dodson, 1999), insects (Cardé and Bell, 1995; Roitberg and Isman, 1992), and vertebrates (Kats and Dill, 1998; Tollrian and Harvell, 1999). Likewise, there is a rich literature on the emission of chemical information by plants and its use by arthropods (Schoonhoven et al., 1998; Chadwick and Goode, 1999), by fungi (Nagashi and Douds, 1999) and by plant-parasitic plants (Estabrook and Yoder, 1998). In addition, allelopathic effects of plant compounds on neighbouring plants have been amply documented (Pellisier and Souto, 1999; Mallik and Romeo, 2000). The role of chemical information in interactions between damaged and undamaged plants, however, remained controversial ever since the first scientific publications appeared in the early 1980s (Baldwin and Schultz, 1983; Rhoades, 1983; Fowler and Lawton, 1985). Some studies found no evidence for transfer of information between damaged and undamaged plants (Myers and Willams, 1984; Williams and Myers, 1984; Fowler and Lawton, 1985; Lin et al., 1990; Preston et al., 1999). Many others presented evidence supporting the hypothesis of information conveyance between damaged and undamaged plants (Rhoades, 1983; Haukioja et al., 1985; Rhoades, 1985; Zeringue, 1987; Dicke et al., 1990; Farmer and Ryan, 1990; Bruin et al., 1992; Shulaev et al., 1997; Arimura et al., 2000; Dolch and Tscharntke, 2000; Karban et al., 2000) and several stimulating reviews have been published in the past five years (Bruin et al., 1995; Shonle and Bergelson, 1995; Karban and Baldwin, 1997).

Yet, studies on plant-to-plant communication are often received with scepticism. The major issues raised by critics are, in random order: (1) data suffer from statistical flaws such as pseudoreplication, (2) the dose of the chemical cues applied in experiments was unrealistically high, (3) the mechanism is unknown or alternative mechanisms may explain the data, (4) ubiquitous cues cannot be meaningful information in interactions between damaged and undamaged plants, and (5) experiments under realistic field conditions are lacking (Fowler and Lawton, 1985; Firn and Jones, 1995; Karban and Baldwin, 1997). Although related to very different aspects of experimental studies, each of these issues is important and should be considered in studies on information conveyance between damaged and undamaged plants. They should stimulate scientists to improve their experimental protocols, to investigate alternative mechanisms, to determine costs and benefits, and to assess the impact on population dynamics—in short they should stimulate continual investigation of a phenomenon with good potential. After all, there is abundant evidence that chemical information from damaged plants is available to undamaged plants.

2. Plants ‘talk’: characteristics of volatiles from damaged plants

In the past two decades it has been well documented that plants respond to damage and herbivory with the emission of a bouquet of volatiles (see e.g. Takabayashi and Dicke, 1996; Chadwick and Goode, 1999; Dicke and Vet, 1999; Sabelis et al., 1999 for reviews). These volatiles are usually emitted in considerable quantities and the bouquet is often dominated by compounds that are not emitted when the plant is undamaged or mechanically damaged (Boland et al., 1999; Dicke, 1999b). In other cases only minor qualitative differences exist in the composition of the blends from mechanically damaged and herbivore-damaged plants (Dicke, 1999b). The blends emitted by herbivore-damaged plants usually contain fatty-acid derivatives and terpenoids, but also nitrogenous compounds, sulphur containing compounds and phenolics such as methyl salicylate are frequently found (Turlings et al., 1995; de Moraes et al., 1998; Boland et al., 1999; Dicke, 1999b). The composition of the blend emitted by damaged plants is specific for the plant species and the herbivore that damages the plant (Takabayashi and Dicke, 1996; de Moraes et al., 1998; Du et al., 1998; Turlings et al., 1998; Dicke, 1999a). It has been well documented that the volatiles emitted by herbivore-damaged plants attract carnivorous enemies of the herbivores (e.g. Turlings et al., 1995; Takabayashi and Dicke, 1996; Dicke and Vet, 1999; Sabelis et al., 1999) and this can benefit the plant in terms of seed production (Van Loon et al., 2000). However, the information is available to all organisms downwind from the infested plant, including downwind plants.

3. Why would plants ‘listen’?

In discussions of communication between plants the emphasis is often placed on the benefits to the emitter. However, given that chemical information from damaged plants is available, the important question is: do downwind neighbours exploit this information to their own benefit? After all, the wind that transfers the information from damaged to undamaged plants can also transport attackers such as pathogens and small herbivores such as mites and insects. The mere presence of damage-related plant compounds implies the vicinity of these attackers, and thus an increased risk of injury to undamaged neighbouring plants. The information available can be specific for the plant-attacking species, which potentially allows plants to discriminate between attackers with different degrees of risk. However, to date it remains unknown whether plants are capable of such discrimination. If not, this will be a constraint for the strategy of the receiving plant.

Plants cannot run away when they are informed that their environment changes into an enemy-dense space, but they could induce a defence. There is ample evidence for inducible defences in plants (Karban and Baldwin, 1997) and several theories describe why and when plants should employ inducible defences rather than constitutive defences (Agrawal and Karban, 1999). One of the potential costs of inducible defence is the time it takes to initiate the defence—it may simply become effective too late. A response to early information on the presence of attackers, such as volatiles from an upwind infested neighbour, could reduce this cost.

4. Past evidence

Various groups have published data that support the hypothesis that chemical information conveyance occurs between damaged and undamaged plants, although shortcomings may still be present (Table 1). Some critics will say that not a single study has met all criteria needed to support the hypothesis for a single system. Several studies have enclosed plants in small airtight bell jars or other types of containers for considerable periods of time (e.g. Farmer and Ryan, 1990; Shulaev et al., 1997; Arimura et al., 2000; Birkett et al., 2000). Under such conditions, plants rapidly deplete the available CO_2, and are forced to photosynthesize below their CO_2 compensation point which causes all kinds of stress (Demeter et al., 1995; Nilsen and Orcutt, 1996; Zobayed et al., 1999). Therefore, conclusions from such studies should be viewed with caution.

Some studies provide carefully designed laboratory studies but have not shown the phenomenon in the field. Zeringue (1987) nicely showed that cotton leaves produce terpenoids after exposure to microbe-filtered air from *Aspergillus flavus*-infested cotton leaves. These laboratory experiments meet many criteria to prove that volatiles from infested plants can affect their downwind neighbours, but a field analysis still needs to be done. Similarly, a well-performed laboratory study shows that volatiles from sagebrush can induce proteinase inhibitors in tomato plants and that the synthetic for one of these volatiles, i.e. methyl jasmonate, has the same effect (Farmer and Ryan, 1990). However, this study lacks ecological reality because tomato and sagebrush do not co-occur in the field. A recent field study shows that undamaged wild tobacco plants next to damaged sagebrush experience reduced feeding damage by naturally occurring herbivores and methyl jasmonate from sagebrush seems to be involved (Karban et al., 2000). Blocking soil contact did not affect the result, but blocking contact through the air did. The latter paper is a good example of how this field should be developed: by taking published papers as a starting point to design new experiments that pay attention to perceived shortcomings. It will provide important building blocks for investigations on the responses of plants to chemical information from damaged neighbours.

5. Variation in plant responses

An important question is whether we expect to find information conveyance between damaged and undamaged plants for all plant species. And if plants of a certain species exhibit the ability, a relevant question is whether individuals of that species should always respond to information from damaged neighbours (Bruin et al., 1995). Such questions are common in other fields related to phenotypic plasticity such as learning in insects (Papaj and Prokopy, 1989; Vet et al., 1995). Can we identify categories of plants that are more likely and categories that are less likely to employ information conveyance between wounded and unwounded plants? For instance, perennial plants may be exposed much more frequently to herbivores than annuals and annuals are thought to be under strong selection to grow quickly at the expense of investing in defence (Herms and Mattson, 1992). Therefore, it may be hypothesized that phenotypic plasticity in responses towards chemical information from neighbours occurs more frequently among herbaceous plants than trees. An even more interesting question is whether individual plants show variation in the

Table 1
Studies published before 2001 that have presented evidence in favour of the hypothesis that chemical information from damaged plants affects undamaged neighbours

System investigated	Field/ laboratory study	Evidence presented	Main weakness	Next step needed	Reference
Sitka willow *Malacosoma californicum pluviale* (caterpillar)	Field	Foliage from plants in the neighbourhood of caterpillar damaged plants has lower food quality for caterpillars than foliage from distant control plants. Soil communication excluded in one experiment.	Pseudoreplication. An entomopathogen may explain the results.	Make replications. Repeat with mechanically damaged trees to avoid the entomopathogen problem (see Haukioja et al., 1985). Or investigate whether pathogens are present and assess how they affect the caterpillars	Rhoades (1983)
Sitka willow *Hyphantria cunea* (caterpillar)	Field	Foliage from plants in the neighbourhood of caterpillar damaged plants has lower food quality for caterpillars than foliage from distant control plants.	Pseudoreplication. Mechanism unknown.	Investigate mechanism.	Rhoades (1983)
Poplar Sugar maple Mechanical damage	Laboratory	Increased phenolic levels in plants exposed to volatiles from damaged conspecifics in the same room.	One room for treatment and one room for control. Pseudoreplication.	Increase number of replicates (rooms). Analyse volatiles and investigate which of the them are involved.	Baldwin and Schultz (1983)
Mountain birch *Epirrita autumnata* (caterpillar)	Field	Growth, survival and reproduction of caterpillars fed on field-collected leaves is positively correlated with distance of tree from closest tree defoliated in previous year.	Mechanism unknown.	Investigate mechanism and variation in plant response.	Haukioja et al. (1985)
Cotton *Aspergillus flavus* (fungus)	Laboratory	Increased concentration of terpenoids in leaves exposed to microbe-filtered air from fungus-infected leaves. No effect of exposure to volatiles from liquid fungus culture or mechanically damaged leaves.	Detached leaves were used instead of whole plants.	Use plants instead of detached leaves. Laboratory experiments on variation in plant response. Field experiments.	Zeringue (1987)
Barley *Erisyphe graminis* f.sp. *hordei*	Laboratory	Barley seedlings placed in the same container as pruned barley seedlings had increased	Pseudoreplication and mechanism unknown.	Increase number of replicates and elucidate mechanism.	Fujiwara et al. (1987)

Table 1 (*continued*)

System investigated	Field/ laboratory study	Evidence presented	Main weakness	Next step needed	Reference
(fungus)		resistance to powdery mildew compared to seedlings incubated with undamaged seedlings.			
Sagebrush Tomato Methyl jasmonate	Laboratory	Induction of proteinase inhibitors in tomato plants exposed to sagebrush branches or synthetic methyl jasmonate in small containers.	Laboratory study on an artificial system.	Field study with naturally co-occurring plants (see Karban et al., 2000).	Farmer and Ryan (1990)
Lima bean *T. urticae* (herbivorous mite) *P. persimilis* (carnivorous mite)	Laboratory	Exposure of plants to volatiles from spider mite-infested conspecifics leads to attraction of predatory mites that prey on spider mites.	Only results from two replicates published, although data from four replicates are available by now (Bruin et al., unpublished data). Results may be explained by adsorption of predator attractants on receiving plants.	Demonstrate that volatiles from infested plants affect gene expression in exposed uninfested plants (see Arimura et al., 2000).	Dicke et al. (1990)
Cotton *T. urticae* (herbivorous mite) *P. persimilis* (carnivorous mite)	Laboratory	Exposure of plants to volatiles from spider mite-infested conspecifics leads to (a) reduced reproductive success of spider mites and (b) attraction of predatory mites that prey on spider mites.	In (a): Direct effect of volatiles from infested plant may affect spider mite feeding behaviour on downwind plants and consequently reproductive success. In (b): Volatiles from infested plants may have been adsorbed onto receiving plants.	Demonstrate that volatiles from infested plants affect gene expression in exposed uninfested plants (see Arimura et al., 2000).	Bruin et al. (1992)
Lima bean Cucumber *T. urticae* (herbivorous mite) *P. persimilis* (carnivorous mite)	Laboratory	Exposure of undamaged cucumber plants to volatiles from spider-mite infested Lima bean plants resulted in attraction of predatory mites that prey on spider mites.	Only two replicates.	Increase number of replicates.	Oudejans and Bruin (1995)

Tobacco Tobacco Mosaic Virus Methyl salicylate	Laboratory	Exposure of undamaged tobacco plant to volatiles from TMV-infected tobacco plant results in induction of PR-1 gene expression and reduction in lesion diameter after infection with TMV. Exposure to mock-infected plants has no effects. Separate experiments to investigate the role of methyl salicylate.	Only two replicates of communication experiment. Experiments with methyl salicylate use very high doses.	Increase number of replicates.	Shulaev et al. (1997)
Lima bean *T. urticae* (herbivorous mite)	Laboratory	Confinement of spider-mite infested leaves in the same container as uninfested leaves results in expression of several defensive genes (PAL, FPS, LOX and PR-genes).	Detached leaves were used.	Use plants instead of detached leaves. Field experiments.	Arimura et al. (2000)
Nicotiana attenuata Grasshoppers Noctuid moths	Field	Wild tobacco plants with clipped sagebrush neighbours had increased levels of polyphenol oxidase and reduced levels of leaf damage by grasshoppers and cutworms relative to control plants with unclipped sagebrush neighbours.	Tobacco plants transplanted to proximity of sagebrush.	Establish the exact involvement of methyl jasmonate.	Karban et al. (2000)
Vicia faba (*Z*)-jasmone *Aphidius ervi* (parasitoid)	Laboratory and field	Exposure of faba bean plants to (*Z*)-jasmone results in the induction of gene expression and the emission of the terpene (*E*)-β-ocimene and in attraction of the parasitoid.	High dose of (*Z*)-jasmone applied compared to emission rate. Experiments using the natural odour source (aphid-infested faba bean plants) should be carried out.	Use aphid-infested plants and natural dose of (*Z*)-jasmone. Extend field study to incorporate natural transfer of (*Z*)-jasmone from infested to uninfested plants.	Birkett et al. (2000)
Alnus glutinosa *Agelastica alni* (herbivorous beetle)	Field	Manual defoliation of 20% of foliage of individual trees results in reduced herbivory in neighbouring trees. The effect wanes with distance from defoliated tree and with time since defoliation.	Mechanism unknown.	Elucidate mechanism.	Dolch and Tscharntke (2000)

expression of induced responses to chemical information from injured neighbours and what causes this variation. For instance, nutrient availability may affect plant investments in defence relative to investments in growth (Herms and Mattson, 1992), age may determine whether an annual plant still invests in defence or only in reproduction, or previous experiences with attackers may affect the strength of the plant's response. Furthermore, the role of plant-to-plant communication through chemicals is often investigated for interactions between conspecifics (but see Farmer and Ryan, 1990; Oudejans and Bruin, 1995; Karban et al., 2000). However, there is no good argument why plants would not be able to exploit chemical information from heterospecific damaged plants. The topic of strategies of plant responses to chemical information will be exciting for those systems where the plant's response has been demonstrated, but not less for those systems where the plant's response was not found. Thinking in terms of individual plant strategies may help in following up studies that did not find a plant response.

6. Above versus below-ground transfer of information

Most research on interactions between damaged and undamaged plants addresses the role of plant volatiles (Bruin et al., 1995; Shonle and Bergelson, 1995; Karban and Baldwin, 1997) and specific experiments have been designed to exclude below-ground communication (Zeringue, 1987; Farmer and Ryan, 1990; Bruin et al., 1992; Karban et al., 2000). However, interactions between plants and other organisms may also be mediated by chemical information in root exudates (Estabrook and Yoder, 1998). One study on information conveyance between damaged and undamaged plants may be explained by below-ground effects (Haukioja et al., 1985). Although interesting in itself, the medium of communication is of course not the main topic if one asks whether communication between damaged and undamaged plants occurs at all and how this affects the ecology of plant–attacker interactions. In fact, the underground transfer of information may be facilitated by root networks and by mycorrhizal connections that may transport nutrients (Simard et al., 1997) and potentially also elicitors of defence over considerable distances.

7. Comparison with research on the use of chemical information by animal receivers

In the study of chemical information transfer between plants, much can be learned from research on chemical information in interactions between animals. Optimal foraging theory assumes that animals are omniscient and take optimal decisions accordingly (Stephens and Krebs, 1986). Although this assumption has often been criticized as being unrealistic, there is growing evidence that animals exploit many sources of information to adjust their behavioural decisions (e.g., Milinski, 1990; Janssen et al., 1997; Tollrian and Harvell, 1999; Dicke and Van Loon, 2000). This includes information on resources, competitors and natural enemies. Research on the role of chemical information in interactions between animals has bloomed during the past decennia. The roles of alarm pheromones and predator-produced kairomones have been well-studied (Pickett et al., 1992; Kats and Dill, 1998; Tollrian and Harvell, 1999). Recurring elements in studies on chemical information conveyance between animals are (1) behavioural data on pheromone emission, e.g. on exposure of glands; (2) behavioural data on response to pheromones, where in the experimental design the receiver is usually deprived of other sensory modalities, such as vision or hearing; (3) chemical analysis of the information conveying compounds; (4) electrophysiological data on perception of identified compounds; (5) confirmation of laboratory data in the field (Shorey, 1976; Roitberg and Isman, 1992; Cardé and Bell, 1995). Subsequently, variation in the production of and response to animal pheromones can be studied.

Analogous to the reasoning for animals, plants should also be expected to be omniscient about prevailing conditions, notwithstanding the fact that they lack a nervous system. And the evidence for plants being informed about their environment is accumulating. For instance, plants can exploit chemical elicitors from their attackers (Mattiacci et al., 1995; Alborn et al., 1997), chemical cues from their resources (Estabrook and Yoder, 1998), or visual signals from their neighbouring competitors (Ballaré, 1999). With regard to infochemicals that mediate plant–plant interactions, it seems that research cannot provide component (1) of evidence generated for information conveyance between animals. Still, an analysis of dynamics of stomata opening and gland activities might reveal interesting data. Although it will be very interesting to study behavioural responses of plants to volatile compounds (cf. component 2), research on information transfer between plants is more likely to provide evidence on physiological responses in the receiving plant. Electrophysiological investigations of plant responses to volatiles from neighbours (cf. component 4) may seem to be unrealistic (but see Wildon et al., 1992). Plant pheromone studies should supply data on (a) the emission of volatiles from damaged plants, (b) the physiological response of plants in experiments where the transfer of other information or agents (pathogens for instance) is excluded and where plants do not suffer from other stresses, (c) the identity of the compounds transferring information, (d) the effect on herbivores and their natural enemies and plant fitness, and (e) the existence of the phenomenon in the field. Of course, a single study does not have to present all these data together. Just as in research on chemical information conveyance between animals, studies can complement each other. Once evidence for plant-to-plant communication has been found, it becomes feasible to investigate to what extent plants are informed about local conditions and what strategies they can follow (Karban et al., 1999).

8. Contributions to this special issue

Considering the importance of chemical information in the ecology of protozoa, invertebrate and vertebrate animals (Roitberg and Isman, 1992; Cardé and Bell, 1995; Kats and Dill, 1998; Kuhlmann et al., 1999; Tollrian and Harvell, 1999) and plant-parasitic plants (Estabrook and Yoder, 1998), it is important to investigate whether and how plants can perceive chemicals from damaged neighbours. At present the research field of plant-to-plant communication is mostly involved in such mechanistic issues. However, evolutionary questions should also be addressed, so as to better understand plant strategies, which may in turn have a stimulating effect on subsequent mechanistic studies. This special issue brings together new experimental evidence on information transfer between plants. All contributors have been asked to address the following questions:

1. Describe (new) experimental evidence on information transfer from wounded to unwounded plants. What were the incentives to study plant–plant communication in this system?
2. How strong is the evidence in favour of information transfer in "your" system? Discuss why alternative options cannot explain the results.
3. What are the most important questions to be answered next?
4. Do you consider plant–plant interactions to be important in nature?

The authors provide important new building blocks for the further development of the research field of plant-to-plant communication. For two systems for which support for chemical information transfer between plants in the field has been recently published (Dolch and Tscharntke, 2000; Karban et al., 2000) additional data are presented. New evidence on communication in the field between sagebrush and wild tobacco and assessment of the potential role of *cis*-methyl jasmonate is presented (Karban, 2001; Preston et al., 2001). Field data on communication between alder trees (Dolch and Tscharntke, 2000) are followed up by laboratory investigations on the underlying mechanism (Tscharntke et al., 2001). Additional data on gene expression in lima bean plants exposed to individual volatiles from herbivore-infested neighbouring plants are presented (Arimura et al., 2001). Furthermore, information is presented on belowground communication among aphid-infested and uninfested faba bean plants (Chamberlain et al., 2001) and among spider-mite infested and uninfested lima bean plants (Dicke and Dijkman, 2001). Finally new avenues for research in this exciting field are identified (Bruin and Dicke, 2001).

This special issue is meant to provide an up-to-date account of this exciting research field and to stimulate the initiation of new research projects. These hopefully are not only restricted to mechanistic, but also to evolutionary questions.

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References

Agrawal, A., Karban, R., 1999. Why induced defenses may be favored over constitutive strategies in plants. In: Tollrian, R., Harvell, C.D. (Eds.), The Ecology and Evolution of Inducible Defenses. Princeton University Press, Princeton, N.J, pp. 45–61.

Alborn, T., Turlings, T.C.J., Jones, T.H., Steinhagen, G., Loughrin, J.H., Tumlinson, J.H., 1997. An elicitor of plant volatiles from beet armyworm oral secretion. Science 276, 945–949.

Arimura, G., Ozawa, R., Horiuchi, J., Nishioka, T., Takabayashi, J., 2001. Plant-plant interactions mediated by volatiles emitted from plants infested by spider mites. Biochem. Syst. Ecol. 29, 1049–1061.

Arimura, G., Ozawa, R., Shimoda, T., Nishioka, T., Boland, W., Takabayashi, J., 2000. Herbivory-induced volatiles elicit defence genes in lima bean leaves. Nature 406, 512–515.

Baldwin, I.T., Schultz, J.C., 1983. Rapid changes in tree leaf chemistry induced by damage: evidence for communication between plants. Science 221, 277–279.

Ballaré, C.L., 1999. Keeping up with the neighbours: phytochrome sensing and other signalling mechanisms. Trends Plant Sci. 4, 97–102.

Birkett, M.A., Campbell, C.A.M., Chamberlain, K., Guerrieri, E., Hick, A., Martin, J.L., Matthes, M., Napier, J.A., Pettersson, J., Pickett, J.A., Poppy, G.M., Pow, E.M., Pye, B.J., Smart, L.E., Wadhams, G.H., Wadhams, L.J., Woodcock, C.M., 2000. New roles for *cis*-jasmone as an insect semiochemical and in plant defense. Proc. Natl Acad. Sci. USA 97, 9329–9334.

Boland, W., Koch, T., Krumm, T., Piel, J., Jux, A., 1999. Induced biosynthesis of insect semiochemicals in plants. In: Chadwick, D.J., Goode, J. (Eds.), Insect–Plant Interactions and Induced Plant Defence, Novartis Foundation Symposium 223. Wiley, Chicester, pp. 110–126.

Bruin, J., Dicke, M., 2001. Chemical information transfer between wounded and unwounded plants: backing up the future. Biochem. Syst. Ecol. 29, 1103–1113.

Bruin, J., Dicke, M., Sabelis, M., 1992. Plants are better protected against spider-mites after exposure to volatiles from infested conspecifics. Experientia 48, 525–529.

Bruin, J., Sabelis, M.W., Dicke, M., 1995. Do plants tap SOS signals from their infested neighbours? Trends Ecol. Evol. 10, 167–170.

Cardé, R.T., Bell, W.J. (Eds.), 1995. Chemical Ecology of Insects 2. Chapman and Hall, New York.

Chadwick, D.J., Goode, J.A. (Eds.), 1999. Insect–Plant Interactions and Induced Plant Defence, Novartis Foundation Symposium 223,. Wiley, Chicester.

Chamberlain, K., Guerrieri, E., Pennacchio, F., Pettersson, J., Pickett, J.A., Poppy, G.M., Powell, W., Wadhams, L.J., Woodcock, C.W., 2001. Can aphid-induced plant signals be transmitted aerially and through the rhizosphere? Biochem. Syst. Ecol. 29, 1063–1074.

Demeter, S., Janda, T., Kovacs, L., Mende, D., Wiessner, W., 1995. Effects of in-vivo CO_2-depletion on electron-transport and photoinhibition in the green algae, *Chlamydobotrys stellata and Chlamydomonas reinhardtii*. Biochim. Biophys. Acta-Bioenergetics 1229, 166–174.

de Moraes, C.M., Lewis, W.J., Paré, P.W., Alborn, H.T., Tumlinson, J.H., 1998. Herbivore-infested plants selectively attract parasitoids. Nature 393, 570–573.

Dicke, M., 1999a. Are herbivore-induced plant volatiles reliable indicators of herbivore identity to foraging carnivorous arthropods? Entomol. Exp. Appl. 92, 131–142.

Dicke, M., 1999b. Evolution of induced indirect defense of plants. In: Tollrian, R., Harvell, C.D. (Eds.), The Ecology and Evolution of Inducible Defences. Princeton University Press, Princeton, NJ, pp. 62–88.

Dicke, M., Dijkman, H., 2001. Within-plant circulation of systemic elicitor of induced defence and release from roots of elicitor that affects neighbouring plants. Biochem. Syst. Ecol. 29, 1075–1087.

Dicke, M., Sabelis, M.W., Takabayashi, J., Bruin, J., Posthumus, M.A., 1990. Plant strategies of manipulating predator–prey interactions through allelochemicals: prospects for application in pest control. J. Chem. Ecol. 16, 3091–3118.

Dicke, M., Van Loon, J.J.A., 2000. Multitrophic effects of herbivore-induced plant volatiles in an evolutionary context. Entomol. Exp. Appl. 97, 237–249.

Dicke, M., Vet, L.E.M., 1999. Plant–carnivore interactions: evolutionary and ecological consequences for plant, herbivore and carnivore. In: Olff, H., Brown, V.K., Drent, R.H. (Eds.), Herbivores: Between Plants and Predators. Blackwell Science, Oxford, UK, pp. 483–520.

Dolch, R., Tscharntke, T., 2000. Defoliation of alders (*Alnus glutinosa*) affects herbivory by leaf beetles on undamaged neighbours. Oecologia 125, 504–511.

Du, Y., Poppy, G.M., Powell, W., Pickett, J.A., Wadhams, L.J., Woodcock, C.M., 1998. Identification of semiochemicals released during aphid feeding that attract parasitoid *Aphidius ervi*. J. Chem. Ecol. 24, 1355–1368.

Estabrook, E.M., Yoder, J.I., 1998. Plant–plant communications: rhizosphere signaling between parasitic angiosperms and their hosts. Plant Physiol. 116, 1–7.

Farmer, E.E., Ryan, C.A., 1990. Interplant communication: airborne methyl jasmonate induces synthesis of proteinase inhibitors in plant leaves. Proc. Natl Acad. Sci. USA 87, 7713–7716.

Firn, R.D., Jones, C.G., 1995. Plants may talk, but can they hear? Trends Ecol. Evol. 10, 371.

Fowler, S.V., Lawton, J.H., 1985. Rapidly induced defenses and talking trees: the devil's advocate position. Am. Nat 126, 181–195.

Fujiwara, M., Oku, H., Shiraishi, T., 1987. Involvement of volatile substances in systemic resistance of barley against *Erisyphe graminis* f. sp. *hordei* induced by pruning of leaves. J. Phytopathol. 120, 81–84.

Haukioja, E., Suomela, J., Neuvonen, S., 1985. Long-term inducible resistance in a birch foliage: triggering cues and efficacy on a defoliator. Oecologia 65, 363–369.

Herms, D.A., Mattson, W.J., 1992. The dilemma of plants: to grow or to defend. Q. Rev. Biol. 67, 283–335.

Janssen, A., Bruin, J., Jacobs, G., Schraag, R., Sabelis, M.W., 1997. Predators use volatiles to avoid prey patches with conspecifics. J. Anim. Ecol. 66, 223–232.

Karban, R., 2001. Communication between sagebrush and wild tobacco in the field. Biochem. Syst. Ecol. 29, 995–1005.

Karban, R., Agrawal, A.A., Thaler, J.S., Adler, L.S., 1999. Induced plant responses and information content about risk of herbivory. Trends Ecol. Evol. 14, 443–447.

Karban, R., Baldwin, I.T., 1997. Induced Responses to Herbivory. Chicago University Press, Chicago.

Karban, R., Baldwin, I.T., Baxter, K.J., Laue, G., Felton, G.W., 2000. Communication between plants: induced resistance in wild tobacco plants following clipping of neighboring sagebrush. Oecologia 125, 66–71.

Kats, L.B., Dill, L.M., 1998. The scent of death: chemosensory assessment of predation risk by prey animals. Ecoscience 5, 361–394.

Kuhlmann, H.-W., Kusch, J., Heckmann, K., 1999. Predator-induced defences in ciliated protozoa. In: Tollrian, R., Harvell, C.D. (Eds.), The Ecology and Evolution of Inducible Defences. Princeton University Press, Princeton, NJ, pp. 142–159.

Lin, H., Kogan, M., Fischer, D., 1990. Induced resistance in soybean to the Mexican bean beetle (Coleptera: Coccinellidae): comparison of inducing factors. Environ. Entomol. 19, 1852–1857.

Mallik, A.U., Romeo, J.T. (Eds.), (2000). Special issue: allelopathy. J. Chem. Ecol. 26, 2007–2241.

Mattiacci, L., Dicke, M., Posthumus, M.A., 1995. Beta-glucosidase: an elicitor of herbivore-induced plant odor that attracts host-searching parasitic wasps. Proc. Natl Acad. Sci. USA 92, 2036–2040.

Milinski, M., 1990. Information overload and food selection. In: Hughes, R.N. (Ed.), Behavioural mechanisms of food selection. Springer, Berlin, pp. 721–736.

Myers, J.H., Willams, K.S., 1984. Does tent caterpillar attack reduce the food quality of red alder foliage? Oecologia 62, 74–79.

Nagashi, G., Douds, D.D., 1999. Rapid and sensitive bioassay to study signals between root exudates and arbuscular mycorrhizal fungi. Biotechnol. Techn. 13, 893–897.

Nilsen, E.T., Orcutt, D.M., 1996. The Physiology of Plants Under Stress. Abiotic Factors. Wiley, New York.

Oudejans, A.M.C., Bruin, J., 1995. Does spider-mite damage induce information transfer between plants of different species? Med. Fac. Landbouww. Univ. Gent. 59, 733–739.

Papaj, D.R., Prokopy, R.J., 1989. Ecological and evolutionary aspects of learning in phytophagous insects. Ann. Rev. Entomol. 34, 315–350.

Pellisier, F., Souto, X.C., 1999. Allelopathy in northern temperate and boreal semi-natural woodland. Crit. Rev. Plant Sci. 18, 637–652.

Pickett, J.A., Wadhams, L.J., Woodcock, C.M., Hardie, J., 1992. The chemical ecology of aphids. Annu. Rev. Entomol. 37, 67–90.

Preston, C.A., Laue, G.. Baldwin, I.T., 2001. Methyl jasmonate is blowing in the wind, but can it act as a plant–plant airborne signal? Biochem. Syst. Ecol. 29, 1007–1023.

Preston, C.A., Lewandowski, C., Enyedi, A.J., Baldwin, I.T., 1999. Tobacco mosaic virus inoculation inhibits wound-induced jasmonic acid-mediated responses within but not between plants. Planta 209, 87–95.

Rhoades, D.F., 1983. Responses of alder and willow to attack by tent caterpillars and webworms: Evidence for pheromonal sensitivity of willows. In: Hedin, P.A. (Ed.), Plant Resistance to Insects. American Chemical Society Symposium Series 208. Washington DC. pp. 55–68.

Rhoades, D.F., 1985. Pheromonal communication between plants. In: Cooper-Driver, G.A., Swain, T., Conn, E.C. (Eds.), Chemically Mediated Interactions between Plants and other Organisms. Recent Advances in Phytochemistry, vol. 19. Plenum Press, New York, pp. 195–218.

Roitberg, B.D., Isman, M.B. (Eds.), (1992). Insect Chemical Ecology. An Evolutionary Approach. Chapman & Hall, New York.

Sabelis, M.W., van Baalen, M., Bakker, F.M., Bruin, J., Drukker, B., Egas, M., Janssen, A.R.M., Lesna, I.K., Pels, B., Van Rijn, P., Scutareanu, P., 1999. The evolution of direct and indirect plant defence against herbivorous arthropods. In: Olff, H., Brown, V.K., Drent, R.H. (Eds.), Herbivores: Between Plants and Predators. Blackwell Science, Oxford, pp. 109–166.

Schoonhoven, L.M., Jermy, T., Van Loon, J.J.A., 1998. Insect–Plant Biology. From Physiology to Evolution. Chapman & Hall, London.

Shonle, I., Bergelson, J., 1995. Interplant communication revisited. Ecology 76, 2660–2663.

Shorey, H.H., 1976. Animal Communication by Pheromones. Academic Press, New York.

Shulaev, V., Silverman, P., Raskin, I., 1997. Airborne signalling by methyl salicylate in plant pathogen resistance. Nature 385, 718–721.

Simard, S.W., Perry, D.A., Jones, M.D., Myrold, D.M., Durall, D.M., Molina, R., 1997. Net transfer of carbon between ectomycorrhyzal tree species in the field. Nature 388, 579–582.

Stephens, D.W., Krebs, J.R., 1986. Foraging Theory. Princeton University Press, Princeton.

Takabayashi, J., Dicke, M., 1996. Plant–carnivore mutualism through herbivore-induced carnivore attractants. Trends Plant Sci. 1, 109–113.

Tollrian, R., Dodson, S.I., 1999. Inducible defenses in Cladocera: constraints, costs and multipredator environments. In: Tollrian, R., Harvell, C.D. (Eds.), The Ecology and Evolution of Inducible Defences. Princeton University Press, Princeton, NJ, pp. 177–202.

Tollrian, R., Harvell, C.D. (Eds.), 1999. The Ecology and Evolution of Inducible Defenses. Princeton University Press, Princeton NJ.

Tscharntke, T., Thiessen, S., Dolch, R., Boland, W., 2001. Herbivory, induced resistance, and interplant signal transfer in Alnus glutinosa. Biochem. Syst. Ecol. 29, 1025–1047.

Turlings, T.C.J., Bernasconi, M., Bertossa, R., Bigler, F., Caloz, G., Dorn, S., 1998. The induction of volatile emissions in maize by three herbivore species with different feeding habits: possible conseqences for their natural enemies. Biol. Control 11, 122–129.

Turlings, T.C.J., Loughrin, J.H., McCall, P.J., Rose, U.S.R., Lewis, W.J., Tumlinson, J.H., 1995. How caterpillar-damaged plants protect themselves by attracting parasitic wasps. Proc. Natl Acad. Sci. USA 92, 4169–4174.

Van Loon, J.J.A., De Boer, J.G., Dicke, M., 2000. Parasitoid–plant mutualism: parasitoid attack of herbivore increases plant reproduction. Entomol. Exp. Appl. 97, 219–227.

Vet, L.E.M., Lewis, W.J., Carde, R.T., 1995. Parasitoid foraging and learning. In: Carde, R.T., Bell, W.J. (Eds.), Chemical Ecology of Insects, vol. 2. Chapman & Hall, New York, pp. 65–101.

Wildon, D.C., Thain, J.F., Minchin, P.E.H., Gubb, I.R., Reilly, A.J., Skipper, Y.D., Doherty, H.M., O'Donell, P.J., Bowles, D.J., 1992. Electrical signalling and systemic proteinase inhibitor induction in the wounded plant. Nature 360, 62–65.

Williams, K.S., Myers, J.H., 1984. Previous herbivore attack of red alder may improve food quality for fall webworm larvae. Oecologia 63, 166–170.

Zeringue Jr., H.J., 1987. Changes in cotton leaf chemistry induced by volatile elicitors. Phytochemistry 26, 1357–1360.

Zobayed, S.M.A., Armstrong, J., Armstrong, W., 1999. Evaluation of a closed system, diffusive and humidity-induced convective throughflow ventilation on the growth and physiology of cauliflower in vitro. Plant Cell Tissue Organ Culture 59, 113–123.