ELSEVIER

Research Focus

Plants talk, but are they deaf?

Marcel Dicke[1], Anurag A. Agrawal[2] and Jan Bruin[3]

[1]Laboratory of Entomology, Wageningen University, PO Box 8031, NL-6700 EH Wageningen, The Netherlands
[2]Department of Botany, University of Toronto, 25 Willcocks Street, Toronto, ON, Canada M5S 3B2
[3]Section Population Biology, University of Amsterdam, Kruislaan 320, 1098 SM Amsterdam, The Netherlands

Plants actively respond to damage with the induction of defences. One of these defences involves emitting volatiles that attract the enemies of the enemies of the plant. Whether downwind neighbouring plants 'eavesdrop' on these cues and respond with the induction of their defences too has been debated intensively. Evidence in support of this hypothesis has been accumulating recently, provoking exciting mechanistic and ecological questions that need to be addressed.

Humans often consider plants to be passive organisms, even though individual plants display directed responses to resources such as light and nutrients. Such responses have recently been interpreted as behaviour or foraging in plants [1]. It is also now well established that plants actively respond to arthropod herbivory by producing toxins in leaves and with the emission of volatile chemicals that are exploited by herbivores and carnivores [2–4]. The emission of volatile chemicals has been referred to as the ability of plants to 'talk', that is, to emit information about their state of attack. Although the behavioural responses of plant-inhabiting animals to such chemical information have reached textbook status, there are continuing expressions of scepticism about the ability of plants to respond to damage-related signalling from their neighbours. Plants are still often thought to be 'deaf' to the chemical information emitted by neighbouring plants.

Plants 'talk'

There has been scepticism about plants responding to information from their damaged neighbours ever since it was first reported [5,6]. However, convincing evidence demonstrating plant responses to such information has accumulated over the past 20 years, with major advances in recent years [3,7–9]. The evidence relates to two types of responses by the 'listening' plants: the induction of a direct defence that makes them resistant to subsequent herbivore attack and an indirect defence that involves the recruitment of carnivorous arthropods as 'bodyguards'. Given that plants universally emit induced volatiles in response to herbivory [4], it is apparent that undamaged neighbours could benefit from exploiting this information (Fig. 1). Plants that are able to activate their defences in response to the information from their neighbour might time their defence more effectively and thus gain a selective advantage over plants that are deaf to the information

of their neighbour. Here we highlight the most convincing recent data that support the hypothesis that plants can adaptively respond to the chemical information emitted by their neighbours.

Plants 'listen': evidence from field studies

The most frequent criticism of the plant-to-plant communication hypothesis is that the phenomenon has been documented only from highly artificial laboratory experiments where plants have been enclosed in small containers. However, in recent carefully designed and well-replicated field experiments, partial defoliation of alder (*Alnus glutinosa*) trees resulted in induced resistance in the defoliated trees as well as in their conspecific neighbours [10]. The effects waned with distance from the defoliated tree and with time since defoliation. More mechanistic data collected in laboratory experiments have identified the potential chemical signals and responses that mediated this phenomenon [10,11].
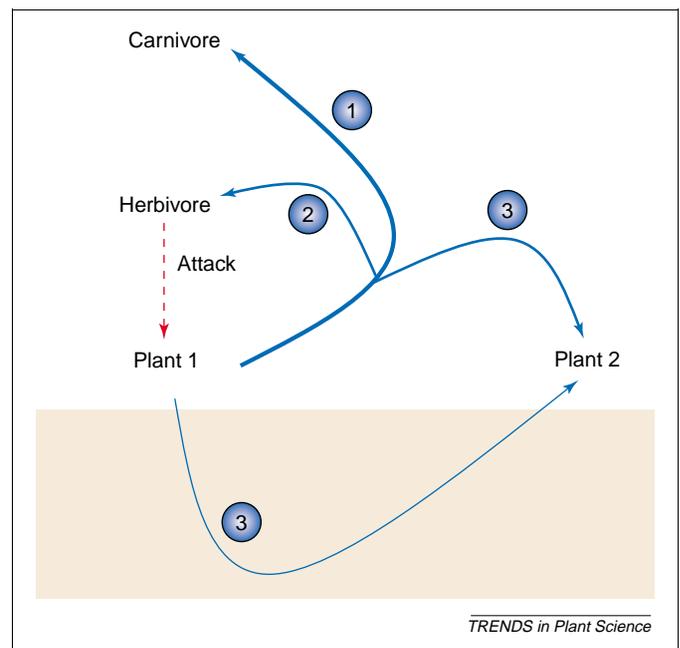

TRENDS in Plant Science

Fig. 1. Plants respond to herbivory with the emission of chemical cues above and below ground, which can elicit responses in (1) carnivorous enemies of the herbivores, (2) herbivores and (3) neighbouring plants. The plant–plant interactions comprise interactions among conspecifics and heterospecifics. The red broken arrow represents herbivore attack on a plant; the blue arrows represent the emission of chemical cues that affect other organisms. The thickness of the blue arrows indicates the relative knowledge of the interactions.

Corresponding author: Marcel Dicke (marcel.dicke@wur.nl).

Recent field evidence extends to the fitness consequences of interspecific plant–plant communication. Native wild tobacco plants that grew next to damaged sagebrush (*Artemisia tridentata*) plants had higher levels of the defensive enzyme polyphenol oxidase and reduced levels of insect damage compared with control plants next to undamaged sagebrush plants [12,13]. Over five years of experiments, tobacco plants next to damaged sagebrush produced more flowers and seed-bearing capsules but were also more susceptible to frost damage compared with controls [14]. However, there was a negative correlation between tobacco capsule production and distance from sagebrush, indicating that sagebrush has an overall detrimental effect on the fitness of tobacco plants. The strength of these studies is that they link chemical mechanisms to processes in natural environments and ultimately address the fitness consequences of the plant–plant interaction.

Plants 'listen': evidence from gene-expression studies

An excellent demonstration of the elaborate and fine-tuned responses of plants to volatile information from their neighbours comes from the assessment of gene expression in a laboratory study. Lima bean (*Phaseolus lunatus*) plants induce the expression of several defence-related genes in response to exposure to individual odours that are emitted from spider-mite damaged conspecific plants [15]. This development opens exciting avenues for future research, such as the monitoring of spatial patterns in gene expression in fields with incipient outbreaks of pests. This will promote an understanding of the spatial spread of defence induction in the field and potentially lead to advances in how to manipulate plant defences in agroecosystems.

Underground signalling between plants

In some of the studies on plant–plant communication, experimental manipulations have specifically addressed whether the communication occurs above ground through volatiles and/or through exchange of information underground [6,12]. However, most studies have concentrated on the role of above-ground volatiles [3,7]. Two recent studies have shown that below-ground information exchange can mediate plant-to-plant communication. Bean plants that were exposed to rhizosphere components from conspecific plants that had been damaged by aphids or spider mites were more attractive to carnivorous enemies of the herbivores [16,17]. Given that studies on plant–arthropod interactions have mostly concentrated on above-ground interactions [18], investigations underground might significantly contribute to our understanding of plant–plant communication. For example, the connections of unrelated plants underground via mycorrhizal networks might be a major thoroughfare by which information is exchanged in plant–plant interactions [19].

Future challenges

Current information on the interactions mediated by chemical signals from wounded plants is presented in Fig. 1. A recurring finding is that not all studies have demonstrated that plants respond to volatiles from their wounded neighbours. Although it might be fashionable in some scientific disciplines to disregard variability, ecologists are charged with unraveling and embracing variability in nature. For example, behavioural ecologists have come to expect variation in the responses of animals to chemical information. Moreover, phenotypic plasticity, the ability to express different phenotypes depending on the biotic and abiotic environment, is a general biological phenomenon that contributes to the variability we observe in interactions [20]. It seems likely that not all plants are deeply involved in chemically mediated dialogues. However, there is strong evidence that plants can and do exploit information from damaged neighbours. Our challenge is to determine the ecological circumstances and abiotic conditions where such plant–plant interactions are common. Rather than closing the discussion on plant–plant communication, the recent advances open the road to exciting new investigations. Major questions include: how do plants perceive the volatile chemicals emitted by their neighbours, what and where are the receptors, can plants discriminate between different volatile blends, what are the constraints on expressing such plant responses, when should plants respond to damage-related volatiles emitted by their neighbour and when should they not? After 20 years of scepticism, it is time to listen to the evidence and move forward.

References

1 Silvertown, J. and Gordon, D.M. (1989) A framework for plant behavior. *Annu. Rev. Ecol. Syst.* 20, 349–366
2 Farmer, E.E. (2001) Surface-to-air signals. *Nature* 411, 854–856
3 Karban, R. and Baldwin, I.T. (1997) *Induced Responses to Herbivory*, Chicago University Press, Chicago, IL, USA
4 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
5 Rhoades, D.F. (1983) Responses of alder and willow to attack by tent caterpillars and webworms: evidence for pheromonal sensitivity of willows. In *In Plant Resistance to Insects* In *American Chemical Society Symposium Series 208, Washington, D.C., USA* (Hedin, P.A., ed.), pp. 55–68
6 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
7 Dicke, M. and Bruin, J. (2001) Chemical information transfer between plants: back to the future. *Biochem. Syst. Ecol.* 29, 981–994
8 Baldwin, I.T. *et al.* (2002) Volatile signaling in plant–plant-herbivore interactions: what is real? *Curr. Opin. Plant Biol.* 5, 351–354
9 Pickett, J.A. *et al.* (2003) Plant stress signalling: understanding and exploiting plant–plant interactions. *Biochem. Soc. Trans.* 31, 123–127
10 Dolch, R. and Tscharntke, T. (2000) Defoliation of alders (*Alnus glutinosa*) affects herbivory by leaf beetles on undamaged neighbours. *Oecologia* 125, 504–511
11 Tscharntke, T. *et al.* (2001) Herbivory, induced resistance, and interplant signal transfer in *Alnus glutinosa*. *Biochem. Syst. Ecol.* 29, 1025–1047
12 Karban, R. *et al.* (2000) Communication between plants: induced resistance in wild tobacco plants following clipping of neighboring sagebrush. *Oecologia* 125, 66–71
13 Karban, R. *et al.* (2003) Herbivore damage to sagebrush induces resistance in wild tobacco: evidence for eavesdropping between plants. *Oikos* 100, 325–332
14 Karban, R. and Maron, J. (2002) The fitness consequences of interspecific eavesdropping between plants. *Ecology* 83, 1209–1213

15 Arimura, G. *et al.* (2000) Herbivory-induced volatiles elicit defence genes in lima bean leaves. *Nature* 406, 512–515

16 Dicke, M. and 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

17 Guerrieri, E. *et al.* (2002) Plant-to-plant communication mediating in-flight orientation of *Aphidius ervi*. *J. Chem. Ecol.* 28, 1703–1715

18 Van der Putten, W.H. *et al.* (2001) Linking above- and belowground multitrophic interactions of plants, herbivores, pathogens, and their antagonists. *Trends Ecol. Evol.* 16, 547–554

19 Simard, S.W. *et al.* (1997) Net transfer of carbon between ectomycorrhizal tree species in the field. *Nature* 388, 579–582

20 Agrawal, A.A. (2001) Phenotypic plasticity in the interactions and evolution of species. *Science* 294, 321–326

Distinct photoperiodic responses are conferred by the same genetic pathway in *Arabidopsis* and in rice

Frédéric Cremer and George Coupland

Max-Planck-Institut für Züchtungsforschung, Carl-von-Linne-Weg 10, 50829 Cologne, Germany

Plants show diverse responses to daylength. For example, *Arabidopsis* and rice flower in response to long and short days, respectively. A recent comparison of the molecular control of flowering has shown that the proteins that confer these responses are conserved in both species. The function of a central transcriptional regulator, called CONSTANS in *Arabidopsis*, is reversed, so that it activates transcription of a downstream gene in *Arabidopsis* but represses the expression of the orthologous gene in rice. This provides the first indication of how diverse responses to daylength are generated.

Plant development is often synchronized to the changing seasons so that major developmental changes occur at characteristic times of the year. These developmental processes are often initiated at times that anticipate the season in which they are required. For example, leaf abscission and bud dormancy occur in autumn, anticipating the onset of winter conditions. Wightman Garner and Henry Allard first recognized that such seasonal responses are often controlled by daylength (or photoperiod) by studying the control of flowering in Maryland mammoth tobacco (*Nicotiana tabacum*) [1]. They went on to classify plants as short day (SD), long day (LD) or day neutral plants according to their responses to daylength. SD plants, such as Maryland mammoth tobacco, are induced to flower when daylength is shorter than a particular duration, called the critical daylength. By contrast, LD plants are induced to flower when daylength is longer than this critical daylength. *Arabidopsis thaliana* is a quantitative LD plant, flowering earlier when the day length is long than when it is short. Recently, Ryosuke Hayama and colleagues compared the molecular control of flowering by photoperiod in *Arabidopsis* with the SD plant rice (*Oryza sativa*) [2]. They showed that although the components that generate the photoperiodic response in *Arabidopsis*

and rice are conserved, the activity of one of the proteins is altered, generating the reverse response to daylength.

The photoperiodic pathway in *Arabidopsis*…
Many mutants of *Arabidopsis* showing an altered flowering time and an impaired response to daylength have been described [3]. These have been placed within a genetic pathway, the photoperiodic pathway, which controls flowering time in response to daylength. This pathway involves photoreceptors, the circadian clock and an output pathway of the circadian clock centred on the *CONSTANS* (*CO*) gene. The order of action of the known components of this output pathway has been defined (Fig. 1). GIGANTEA (GI), a large nuclear protein of unknown biochemical function, is required to increase *CO* transcription, and the photoreceptors phytochrome A (phyA) and cryptochrome 2 (cry2) appear to activate *CO* at the post-transcriptional level [4–6]. CO, a zinc-finger containing nuclear protein, then activates the transcription of *FLOWERING LOCUS T* (*FT*), which encodes a protein with homology to RAF-kinase inhibitor proteins of animals [7–9].

Genetic and molecular data in *Arabidopsis* support the model shown in Fig. 1. The *gi*, *cry2*, *phyA*, *co* and *ft* mutants are all late flowering under long daylength. The *gi-3* mutant shows decreased expression of *CO* [4], whereas the *gi-3* mutation does not delay flowering of plants overexpressing *CO*. FT mRNA abundance is decreased in the *co* mutant background and increased in *CO* overexpressing plants [4,8,9]. The late flowering of the *cry2* mutant and the early flowering of plants over-expressing *CRY2* under short daylength does not affect the level of *CO* transcript [4], but both *cry2* and *phyA* mutations reduce FT mRNA abundance, suggesting that they act post-transcriptionally to regulate CO protein function [6]. This pathway is proposed to activate flowering only in response to long daylength because the post-transcriptional regulation of *CO* that is required for it to activate *FT* expression occurs in response to light, and circadian clock regulation of *CO* transcription ensures that CO expression and exposure to light coincide

Corresponding author: George Coupland (coupland@mpiz-koeln.mpg.de).