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Review

Airborne plant-plant communication

Keith Chamberlain

Department of Biological Chemistry and Crop Protection, Rothamsted Research, Harpenden, AL5 2JQ, UK.
Email: keith.chamberlain@rothamsted.ac.uk

Abstract

Following the early observations of volatile signalling between plants in the mid-1980s**,** there was much debate concerning the validity of the results and the reality of the phenomenon. The substantial literature that covers more than 25 plant species as emitters and/or receivers of volatile compounds is reviewed. The paper also proposes that the passive sorption of small lipophilic molecules from the vapour phase occurs in all higher plants, although the results of such communication are only observable if there is a measurable response.

Introduction

Talking to plants as a means to improve their health has long been advocated, usually by people with a high public profile but rarely by those with a scientific background. As plants do not have organs that function as ears or mouths the idea that they can hear what might be spoken to them or speak to each other seems ridiculous. However, there are other ways of communicating than by speech. Mankind has long used smoke, flags, hand signals, etc. to indicate their needs and intentions. Many, if not most, animals also use chemical signals, or semiochemicals, that mark trails or territory, intimidate other creatures, warn their conspecifics of danger, indicate their state of sexual readiness, help to find a site for laying eggs or giving birth and that help to locate a source of food, be it animal or vegetable. Insects are particularly renowned for using chemical signals in these ways, and frequently their anatomy is supremely adapted for this purpose, hence the great variety, in shape and size, of insects' antennae which contain the majority of their chemical sensors, especially for the detection of volatile compounds.

Plants emit volatile chemicals that are produced as part of their secondary metabolism, not only from their flowers where they serve to attract pollinating insects (Knudsen *et al*., 2006; Schiestl, 2010; Dudareva *et al*., 2013) but also from their vegetative parts (Dudareva *et al*., 2006; Pichersky *et al*., 2006). These compounds can be simple gases, such as oxygen, ethylene

and water vapour, as well as an array of small lipophilic molecules containing from 5 to 20 carbon atoms that include the so called green-leaf volatiles (C_6 aldehydes, alcohols, and esters), terpenes (C_{10} and C_{15} hydrocarbons) and their derivatives, and phenylpropanoids and benzenoids that are derived from the amino acid phenylalanine (Maffei *et al*., 2011).

Although emitted only in trace amounts from healthy, undamaged plant tissue the green-leaf volatiles, together with some terpenoids, are released by plants in significantly increased amounts during a rapid response to stress caused by mechanical damage, for example producing the familiar smell of new mown grass. The same response is induced by biotic stress which may have many causes including feeding by herbivorous insects and mites on vegetative parts (Hare, 2011) and plant diseases caused by fungi (Piel *et al*., 1997; Kishimoto *et al*., 2008), bacteria (Croft *et al*., 1993; Huang *et al*., 2003; Yi *et al*., 2009) or even viral infections (Eigenbrode *et al*., 2002). The C_6 compounds, which are derived from the cleavage of membrane lipids, mainly linoleic and linolenic acids, by the action of lipoxygenase and other enzymes (D'Auria *et al*., 2007; Scala *et al*., 2013), are released quickly as a result of damage to cell membranes. However, because of their high volatility, they are considered not to be stored in specialised structures such as oil ducts or glandular trichomes, unlike the terpenes that are also emitted rapidly after herbivore feeding (Paré and Tumlinson, 1997; Ormerño and Fernandez, 2012).

The initial emission of volatile compounds by plants in response to herbivory is followed by a second phase of volatile release that may not start until several hours or more after feeding begins but could continue for as long as the attack lasts and maybe longer. The compounds that are emitted at this stage are synthesised *de novo*, by a number of biosynthetic routes, although they may be the same as some of those produced in the rapid response to damage (Paré and Tumlinson, 1999; Kigathi *et al*., 2009). Some insects are known to elicit the synthesis and release of these chemicals by introducing oral secretions into the plant (Mattiaci *et al*., 1995; Alborn *et al*., 1997; Schmelz *et al*., 2009).

Airborne plant-insect interactions

Many of the compounds emitted by plants, following attack by herbivores, have been found to have defensive roles against the herbivores and these may be direct or indirect effects. Direct defence involves volatile compounds that repel or deter other insects, whether of the same or different species, from landing on the emitting plant. For instance, feeding by caterpillars of the tobacco budworm moth, *Heliothis virescens* Fabricius, on the leaves of tobacco plants, *Nicotiana tabacum* L.*,* induces the plant to emit volatiles, particularly during

the scotophase, that are repellent to female moths of the same species seeking oviposition sites (De Moraes *et al*., 2001). Volatile defence compounds have been shown to be induced not only by chewing insects but also by piercing, sucking insects such as thrips and the phloem-feeding aphids, although the blend of volatiles induced by them is usually different to that emitted in response to the chewing insects (Delphia *et al*., 2007; Gosset *et al*., 2009; Blande *et al*., 2010).

Indirect defence occurs when the volatiles released by the plant in response to herbivore feeding serve as attractants for enemies of the herbivore such as predators and parasitoids. Such tritrophic interactions have been reported for many plant species that include *Arabidopsis thaliana* L. (van Poecke and Dicke, 2004), *Brassica oleracea* L. (Agelopoulos and Keller, 1994a; 1994b), *Cucumis sativus* L. (Takabayashi *et al*., 1994*), Gossypium hirsutum* L. (Röse *et al*., 1998), *N. tabacum* L. (De Moraes *et al*., 1998), *Phaseolus lunatus* L. (Shimoda *et al*., 1997), *P. vulgaris* L. (Birkett *et al*., 2003), *Pinus sylvestris* L. (Mumm *et al*., 2003), *Solanum lycopersicum* L. (Farag and Paré, 2002) and *Zea mays* L. (Turlings *et al*., 1990). Furthermore, there are instances when herbivore oviposition on plant leaves induces changes in the emission of volatiles such that egg parasitoids are attracted (Hilker and Meiners, 2006). Indirect defence can also take place below ground as exemplified by the attack of western corn rootworm, *Diabrotica virgifera virgifera* LeConte, on the roots of maize, which induces release of the sesquiterpene (E)-caryophyllene into the soil and so attracts an entomopathogenic nematode that infects and kills this very serious pest of maize (Rasmann *et al*., 2005; Degenhardt *et al*., 2009).

There have been a number of comprehensive reviews of the literature covering plant-insect interactions, in general, over the years, two of the most recent being those by Scala *et al*., (2013) and Das *et al*., (2013), and also some more specifically concerning indirect defence such as those by van Poecke and Dicke (2004) and Heil (2008).

Intraplant signalling

There is considerable evidence that volatile chemicals that act in defence of the plant are induced systemically, undamaged leaves remote from the site of herbivore attack also emitting defensive compounds (Turlings and Tumlinson, 1992; Röse *et al*., 1998; Mattiaci *et al*., 2001). It was assumed that a signal was transmitted through the plant via the vascular system, and there is evidence for this (Gómez and Stuefer, 2006). However, Orians (2005) drew attention to the fact that sometimes the induction was more widespread than expected from the vascular architecture and suggested that volatile compounds emitted from the site of attack induce a similar response in parts of the plant remote from the damage. This was subsequently shown to

be the case in a number of plants including sagebrush, *Artemisia tridentata* Nutt. (Karban *et al.*, 2006), a hybrid poplar, *Populus deltoides* Marshall ×*P. nigra* L., (Frost *et al.*, 2007), Lima bean, *Phaseolus lunatus* L., (Heil and Bueno, 2007), and highbush blueberry, *Vaccinium corymbosum* L. (Rodriguez-Saona *et al.*, 2009).

Only a small mental step is needed to proceed from admitting volatile signalling between different parts of the same plant to accepting the possibility of interplant communication, although in practice evidence for the latter preceded the former.

Interplant signalling

It is only to be expected that neighbouring plants are able to eavesdrop on volatile intraplant signals and, if they have the necessary facility, to respond to the message that those signals are conveying. This is more likely if the neighbours are of the same species, because they are able to respond in exactly the same way as the remote parts of the emitting plant, but it is not necessarily so.

The first observation of plant response to airborne signals from nearby plants under attack by herbivores was reported in 1983 for Sitka willows, *Salix sitchensis* Sanson ex Bong. (Rhoades, 1983). It was found that western tent caterpillars, *Malacosoma californicum pluviale* Dyar, feeding on the leaves of un-infested willow trees in close proximity to caterpillar-infested ones grew much more slowly than those feeding on trees further away and the author suggested that this was due to airborne pheromonal substances. He did, however, conclude his report with the statement, "The burden of proof for such an unprecedented effect should be high, and the foregoing experiments with willows and tent caterpillars cannot be considered to constitute such proof." In laboratory conditions, Baldwin and Schultz (1983) carried out experiments that supported Rhoades' suggestion. Using potted plants of Carolina or Canadian poplar, *Populus canadensis* Moench., taken from a single clonal network, they removed about 7% of total leaf area of some plants by tearing. Analysis showed that both the treated plants and undamaged plants in the same enclosure had increased levels and rates of synthesis of phenolic compounds. Similar results were obtained with seedlings of sugar maple, *Acer saccharum* Marshall, which were undamaged but showed increased levels of phenolics and hydrolysable and condensed tannins in response to damage to neighbouring plants. The authors concluded that an airborne cue originating in damaged tissue may stimulate biochemical changes in neighbouring plants.

Both of these early reports on interplant signalling were met with some scepticism and alternative explanations for the results obtained were published a couple of years later by Fowler and Lawton (1985), who pointed out that the study by Baldwin and Schultz was

statistically flawed and suggested that the results of Rhoades were not due to airborne pheromonal substances but instead to tiny airborne infectious stages of a disease affecting the tent caterpillars. The great 'talking tree' debate continued in the literature for the next ten years or so. Fowler and Lawton (1985) included in their paper the results of an experiment using artificially damaged birch saplings, *Betula pubescens* Ehrh., that provided no evidence of plant-to-plant signalling. However, another study found sound evidence of volatile transfer between Arctic downy birch trees, *Betula pubescens* subsp. *tortuosa,* infested with autumnal moth caterpillars, *Epirrita autumnata* Borkhausen, and healthy trees of the same species, in which the magnitude of the effect decreased with distance from the infested trees (Haukioja *et al*., 1985). Most of the reports that followed supported the idea that volatile chemicals induced by herbivory or fungal infection could have a measurable effect on neighbouring undamaged plants, though there were some in which the results were inconclusive and others that sought and failed to find evidence of such interactions. For example, Lin *et al*. (1990) found no evidence of interplant transfer of inducing signals in soybean, *Glycine max* L., following herbivory by the soybean looper, *Pseudoplusia includens* Walker, on neighbouring conspecifics. Supporting evidence was found in a number of plant species including the following: in cotton, *Gossypium hirsutum* L., undamaged leaves showed a significant increase in heliocides, C_{25} terpenoid aldehydes, following exposure to volatiles from leaves infected with the fungus *Aspergillus flavus* Link (Zeringue, 1987); tobacco aphids showed reduced fecundity when feeding on the leaves of tobacco, *N. tabacum,* that had been exposed to the volatiles from mechanically damaged leaves of tomato, *Solanum lycopersicum* L. (Hildebrand *et al*., 1993); the volatiles from damaged tomato plants also inhibited the in vitro germination of apple pollen (Hamiton-Kemp *et al*., 1991); undamaged cotton plants attracted predatory mites, *Phytoseiulus persimilis* Athias-Henriot, after they were exposed to the volatiles from cotton plants under attack by the herbivorous spider mite *Tetranychus urticae* Koch (Bruin *et al*., 1992).

During the next two decades there were many more reports in the literature that contained generally incontrovertible evidence of plant responses to exogenous volatile compounds or blends emanating from conspecific or heterospecific plants. Table 1 summarises instances of plants responding to the volatile blends emitted by other plants, in which the actual chemicals involved are not identified, and Table 2 shows those plants that have been found to respond to individual compounds, all of which have been detected in the volatile emissions of plants. Included in these tables are instances of priming, that is, when plants demonstrate the

ability to respond more rapidly to subsequent attacks by herbivores or pathogens than to the initial attacks. There are many reports in the literature, reviewed by Frost *et al.* (2008a), of such effects being induced by exogenous volatile signals.

Table 1. Summary of reports of interplant communication since 1995

Receiver plant	Emitter plant	Damage	Receiver response	Lab/ Field	Reference
Achyrachaena mollis Schauer *Lupinus nanus* Douglas ex Benth. *Sinapis alba* L.	*A. mollis* *L. nanus* *S. alba*	mechanical	Varying effects on herbivoryand lifetime fitness depending on genetic relationships (Factorial expt.)	F	Pearse *et al.*, 2012
Alnus glutinosa (L.) Gaertn.	*A. glutinosa*	mechanical	reduced herbivory; reduced oviposition	L & F	Dolch & Tscharntke, 2000
Arabidopsis thaliana L.	*A. thaliana*	mechanical	increased attraction of parasitoid	L	Shiojiri *et al.*, 2012
"	*Magnolia grandiflora* L. (flower)	none	induction of defence related genes	L	Matthes *et al.*, 2011
"	*Phaseolus lunatus* L.	herbivory	upregulation of genes in ethylene and jasmonic acid pathways	L	Zhang *et al.*, 2012
Artemisia tridentata Nutt.	*A. tridentata*	mechanical	reduced herbivory; more branches; more flowers	F	Karban *et al.*, 2006; 2012
Cuscuta pentagona Engelm.	*Solanum lycopersicum* L.	none	directed growth by the obligate, parasitic weed	L	Runyon *et al.*, 2006
"	*Impatiens walleriana* Hook. f.	none	directed growth by the obligate, parasitic weed	L	Runyon *et al.*, 2006
"	*Triticum aestivum* L.	none	directed growth by the obligate, parasitic weed	L	Runyon *et al.*, 2006
Gossypium hirsutum L.	*G. hirsutum*	herbivory	reduced oviposition	L & F	Zakir *et al.*, 2013
Hordeum vulgare L.	*Chenopodium album* L.	none	less acceptable to aphids	L & F	Ninkovic *et al.*, 2009
"	*Cirsium arvense* (L.) Scop. *C. vulgare* (Savi) Ten.	none	less acceptable to aphids; attracts aphid predator	L	Glinwood *et al.*, 2004; Ninkovic & Pettersson, 2003
"	*H. vulgare* (Different cultivars to receiver.)	none	less acceptable to aphids; changes in leaf temperature	L	Pettersson *et al.*, 1999; Ninkovic & Åhman, 2009
Medicago sativa L.	*G. hirsutum*	herbivory	reduced oviposition	L	Zakir *et al.*, 2013
Nicotiana tabacum L.	*N. tabacum*	virus infection	increase in pathogenesis –related genes	L	Shulaev *et al.*, 1997
Nicotiana attenuata Steud.	*A. tridentata*	mechanical	reduced herbivory; increased polyphenol oxidase; priming	F	Karban, 2001; Kessler *et al.*, 2006
Phaseolus lunatus L.	*P. lunatus*	herbivory	attraction of predator;	L	Choh *et al.*, 2004
"	"	herbivory	reduced herbivory; faster growth	F	Heil & Bueno, 2007
"	"	herbivory	secretion of extrafloral	F	Kost & Heil,

			nectar; attraction of parasitoids and predators		2006
"	"	chemically induced	primed for resistance to bacterial pathogen	L	Yi *et al*., 2009
Populus ×euramericana (Dode) Guinier	*P. ×euramericana*	herbivory, mechanical	elevated levels of defence related enzymes	L	Tang *et al*., 2013
Solanum tuberosum L.	*Allium cepa* L.	none	avoidance by aphid, *Myzus persicae* Sulzer	L	Ninkovic *et al*., 2013
Tanacetum cinerariifolium Sch.Bip.	*T. cinerariifolium*	mechanical	enhanced production of pyrethrins I &II	L	Kikuta *et al*., 2011
Zea mays L.	*Z. mays*	herbivory / mechanical	priming against subsequent herbivory	L	Engelberth *et al*., 2004; Ton *et al*., 2006

Table 2. Summary of reports of plants responding to individual volatile compounds

Receiver plant	Volatile compound	Receiver response	Reference
Achyranthes bidentata Blume	methyl jasmonate	increased emission of volatiles	Tamogami *et al*., 2008
Arabidopsis thaliana L.	4,8-dimethyl-1,3,7-nonatriene	upregulation of genes in ethylene and jasmonic acid pathways	Zhang *et al*., 2012
"	(*E*)-2-hexenal	induction of defence related genes; induced resistance to *Botrytis cinerea*	Bate & Rothstein, 1998; Kishimoto *et al*., 2005
"	(*Z*)-3-hexenal	induction of defence related genes; induced resistance to *Botrytis cinerea*	Kishimoto *et al*., 2005
"	(*Z*)-3-hexen-1-ol	induction of defence related genes; induced resistance to *Botrytis cinerea*	Kishimoto *et al*., 2005; Zhang *et al*., 2012
"	(*Z*)-jasmone	aphids repelled and parasitoids attracted	Pickett *et al*., 2007; Bruce *et al*., 2008
"	methyl jasmonate	elevation of defence related enzymes; increased green leaf volatile production	Avdiushko *et al*., 1995
"	myrcene	induction of defence related genes	Godard *et al*., 2008
"	ocimenes (mixture of *E*, *Z* and *allo)*	induction of defence related genes	Godard *et al*., 2008
"	*allo*-ocimene	induction of defence related genes; induced resistance to *Botrytis cinerea*	Kishimoto *et al*., 2005
"	4,8,12-trimethyl-1,3,7,11-trideca-tetraene	upregulation of genes in ethylene and jasmonic acid pathways	Zhang *et al*., 2012
Brassica napus L.	methyl jasmonate	increase in glucosinolates	Doughty *et al*., 1995
Citrus jambhiri Lush.	(*E*)-2-hexenal	induction of defence related genes	Gomi *et al*., 2003
"	(*E*)-2-hexen-1-ol	induction of defence related genes	Gomi *et al*., 2003
"	(*Z*)-3-hexen-1-ol	induction of defence related genes	Gomi *et al*., 2003

Cucumis sativus L.	methyl jasmonate	elevation of defence related enzymes; increased green leaf volatile production	Avdiushko *et al*., 1995
Gossypium hirsutum L.	methyl jasmonate	elevated levels of some terpenoids emitted	Rodriguez-Saona *et al*., 2001
Medicago sativa L.	methyl jasmonate	elevation of levels of trypsin inhibitors	Farmer & Ryan, 1990; Farmer *et al*., 1992
Nicotiana tabacum L.	methyl jasmonate	elevation of levels of trypsin inhibitors	Farmer & Ryan, 1990; Farmer *et al*., 1992
"	methyl jasmonate	elevation of defence related enzymes; increased green leaf volatile production	Avdiushko *et al*., 1995
"	methyl salicylate	increase in pathogenesis-related genes	Shulaev *et al., 1997*
Phaseolus lunatus L.	(Z)-3-hexen-1-yl acetate	extrafloral nectar induced	Kost & Heil, 2006
"	methyl salicylate	increased resistance to bacterial pathogen	Girón-Calva *et al*., 2012
"	nonanal	increased resistance to bacterial pathogen	Girón-Calva *et al*., 2012
Populus deltoides ×P. nigra	(Z)-3-hexen-1-yl acetate	priming of defence genes and terpene volatile release	Frost *et al*., 2008b
Populus ×euramericana	benzothiazole	elevated levels of defence related enzymes	Tang *et al*., 2013
Populus ×euramericana	methyl jasmonate	elevated levels of defence related enzymes	Tang *et al*., 2013
Solanum lycopersicum	methyl jasmonate	accumulation of proteinase inhibitors	Farmer & Ryan, 1990; Farmer *et al*., 1992
Populus ×euramericana	methyl salicylate	elevated levels of defence related enzymes	Tang *et al*., 2013
Zea mays L.	(Z)-3-hexenal	jasmonic acid produced; sesquiterpenes emitted	Engelberth *et al*., 2004
"	(Z)-3-hexen-1-ol	jasmonic acid produced; sesquiterpenes emitted	Engelberth *et al*., 2004
"	(Z)-3-hexen-1-yl acetate	jasmonic acid produced; sesquiterpenes emitted	Engelberth *et al*., 2004
Vicia faba L.	(Z)-jasmone	increased levels of terpenoids and attraction of parasitoids	Birkett *et al*., 2000

With more than twenty plant species now identified as receiving and responding to airborne chemicals, there can be little doubt that interplant signalling occurs. However, there remain many unanswered questions. One of these concerns the fitness costs and benefits of the process for both emitter and receiver (Bruin *et al*., 1995; Karban and Maron, 2002; Baldwin *et al*., 2006; Kessler *et al*., 2006; Frost *et al*., 2008a; Dicke and Baldwin, 2010), though in this respect it is important that teleological arguments are avoided. Plants emit volatile chemicals as a means of disposing of the unwanted products of secondary metabolism, membrane disruption, etc., and some of these compounds may then affect the behaviour of plants and insects in the surrounding community. Gases and volatile chemicals enter plants by a passive process of sorption and diffusion across cuticles or directly via stomata and may then be (a) used by the

plant, as in the case of carbon dioxide, (b) metabolised, as any xenobiotic would be, usually as a prelude to disposal via root exudation as a conjugate or by re-volatilisation, or (c) simply re-emitted unchanged. For instance, exogenous, gaseous methyl jasmonate is absorbed by the plant and some is re-emitted unchanged while the remainder enters the symplasm and is metabolised to the plant hormone, jasmonic acid (Tamogami *et al*., 2008).

Sorption of volatile compounds from the atmosphere into the plant cuticle is a partitioning process that, in the absence of any diffusion either through the cuticle or in the air, would reach equilibrium, the concentrations in the two phases depending mainly on the vapour pressure and the lipophilicity of the compound, which is usually measured as the octanol-water partition coefficient (Riederer *et al*., 2002). Since there is considerable movement of the air and diffusion within it, the concentration in that phase will fall quickly and any absorbed compound that has not diffused away from the surface of the cuticle will return to the vapour phase so that equilibrium is restored. In practice, this means that all small lipophilic chemicals in the atmosphere around the plant will not only be sorbed by the plant but also re-emitted to some degree. The re-emission, by the receiving plant, of volatile compounds that originated from the emitting plant was suggested during the great 'talking tree' debate as a possible mechanism for interplant-induced defence (Bruin *et al*., 1995). This was indeed shown to be the case experimentally when undamaged *P. lunatus* was observed to emit a similar blend of volatiles to the one received from conspecifics infested with spider mites, even when the receiver plant was treated with a protein-synthesis inhibitor to stop production of the volatiles (Choh *et al*., 2004). The mechanism also explains the associational resistance to green leaf weevils, *Polydrusus flavipes* De Geer, and birch aphids, *Euceraphis betulae* Koch, in *Betula pendula* Roth and *B. pubescens* growing in mixed associations with *Rhododendron tomentosum* Harmaja. Leaves of the birches were found to adsorb a group of insect repellent sesquiterpenoids emitted by *R. tomentosum* and re-release them into the atmosphere (Himanen *et al*., 2010).

Questions about the range of interplant communications in nature are like those concerning the length of a piece of string as there are many factors to consider. Firstly, there are the properties of the compounds themselves, in particular stability in air, lipophilicity and vapour pressure, which all affect the concentration of the compound in the air and how it will be diluted with distance. Then, there are the weather conditions, which can have a large influence on how the volatiles will behave, especially temperature, strength and direction of any wind and humidity or even rainfall. The density of planting will also have an influence, as the concentration of volatiles in the vapour phase will decrease with each plant that absorbs

them, so that the fewer plants there are between emitter and receiver, the higher will be the concentration that reaches that receiver.

Nonetheless, some reports of field studies include estimates of, or experiments to determine, the distance beyond which the effects are not seen. Many of these studies by Karban and his colleagues concern the emission by clipped sagebrush plants, *A. tridentata,* of volatiles that induce a response in neighbouring plants which are less than 15 cm from the damaged plant in the case of wild tobacco, *Nicotiana attenuata* Steud., (Karban *et al*., 2000; Karban and Maron, 2002) but which can be up to 60 cm away in the case of conspecifics (Karban *et al*., 2006). Preston *et al*. (2004) showed that the concentration of methyl jasmonate in the air above damaged sagebrush was not significantly reduced for at least 40 cm. In a study by Zakir *et al*. (2013), using three different plant species, oviposition by *Spodoptera littoralis* Boisduval was shown to be reduced on plants up to 90 cm from damaged plants of another species. Even greater distances were shown to be possible in stands of alder trees, *Alnus glutinosa* (L.) Gaertn., where effects were observed in trees up to 10 m away from a defoliated tree (Dolch and Tscharntke, 2000). As these measurements depend on the observation of a detectable response, they should not be taken just as a measurement of distance travelled by the volatile signal but also as a measure of the strength of the response in the receiver plant.

Below ground, plant roots can also emit small lipophilic molecules that are relatively volatile and can therefore travel within the airspaces in the soil, although it is likely that the majority of compounds exuded by roots are more polar, conferring water solubility but not volatility. Root cuticles absorb organic compounds in the same way that above-ground parts of plants do, although in normal circumstances there is here a multi-phase partition involved between the cuticle, the vapour phase, the soil organic matter and an aqueous phase. As plant-plant interactions below ground involve a further sophistication in that common mycelial networks, that form connections between neighbouring plants, can transfer warning signals of pathogen and herbivore attack (Song *et al*., 2010; Babikova *et al*., 2013a; 2013b), the specific contribution of airborne interactions in soil is very difficult to assess and has so far not been studied.

Conclusions

There is no question that most higher plants, if not all, emit volatile chemicals in response to abiotic and biotic stress, in addition to those released into the atmosphere constitutively. Some of these compounds have been shown to affect the behaviour of herbivorous insects and mites, their predators and parasitoids, and even hyperparasitoids. The

physicochemical properties of the compounds, in particular their lipophilicity and vapour pressure, are generally such that they are passively absorbed from the atmosphere by plant cuticles of the same or neighbouring plants, whether they are of the same or different species. The absorbed chemicals may then diffuse into the plant symplasm or be re-emitted into the atmosphere. Thus, there is interplant communication in that a signal is transmitted from one plant to another and probably all species of higher plants participate in this process.

The questions that then arise are (1) whether the receiving plant responds in any way to the absorbed chemicals, as is the case with, for example, methyl jasmonate and cis-jasmone, and (2) if the amount of the compound that enters the receiving plant is sufficient to initiate that response. In case the answer to the second question, regardless of the answer to the first, is negative, then there is no apparent communication, but if the answer to both is affirmative, there is clear evidence of plant-plant communication through the vapour phase. In most cases this may only be measurable in the laboratory and even then only if closed chambers or limited diffusion of headspace vapours are employed. In the field, the observation of plant-plant communication is much more difficult because there are so many factors involved, which is why there are so few reports in the literature. However, a strong defensive response to a small transmitted signal could contribute to the natural protection of crop plants from herbivores. For example, the work of Pettersson and colleagues suggests that planting mixtures of barley varieties instead of monocultures could reduce aphid damage within the crop (Pettersson *et al*., 1999; Ninkovic *et al*., 2002).

If a transmitted signal is too small for practical crop defence purposes, it is possible to boost it by companion planting with species that emit larger amounts of the effective chemical (Pickett *et al*., 2014) or even by application of the compound itself as a defence activator, as has been demonstrated for cis-jasmone (Bruce *et al*., 2003).

The great talking tree debate that followed the early discoveries of airborne plant-plant communication has been assigned to history. Any further debate on the general ecology and mechanisms of plant-plant communication must include discussion on how best to utilise this phenomenon, which is here proposed to be universal, for crop protection and increasing the sustainability of food production.

Acknowledgements

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