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Review

Plant–plant communication mediated by airborne signals: ecological and plant physiological perspectives

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Abstract When exposed to herbivore-infested plant volatiles or volatiles from artificially damaged plants, intact plants enhance their defense against herbivores. This phenomenon is called plant-plant communication. Here, we outline studies on plant-plant communication from both ecological and plant physiological perspectives. Regarding the ecological perspective, we give an overview of studies showing that plant–plant communication affect direct and indirect defense levels of exposed plants, and herbivore performance on exposed plants. Cases of kin selection in plant–plant communications and intra-plant communication via airborne signals are also summarized. Regarding the plant physiological perspective, we give an overview of studies that showed specific responses of receiver plants to a volatile molecular species, to different configurations of a volatile molecular species and to blends of volatiles. Furthermore, we review the signaling pathways involved, priming, sensitivity, and how plants receive volatile compounds in plant–plant communications.

Key words: Plant–plant communications, herbivore-induced plant volatiles (HIPVs), jasmonic acid (JA), salicylic acid (SA), extrafloral nectar (EFN).

Ecology of plant–plant communication

Plant volatiles as infochemicals

In response to damage caused by herbivorous arthropods, plants start emitting so-called herbivore-induced plant volatiles (HIPVs) (Takabayashi and Dicke, 1996). For most plant-herbivore combinations, the blends of HIPVs are not exactly the same as those emitted from mechanically damaged plants. Further, HIPV blends are specific in terms of plant species, plant cultivars, herbivore species, and developmental stages of herbivores (Takabayashi 2014 for review). Thus, a blend of HIPVs contains potential information on “who is currently infested by whom.” Predatory and parasitoid arthropods are known to be attracted to such specific volatile information when searching for their targets (Takabayashi 2014 for review). For example, the larval parasitoid wasp, *Cardiochiles nigriceps*, is attracted by plants (tobacco, maize and cotton) infested by host larvae, *Heliothis virescens*, but not by those infested by nonhost larvae, *Helicoverpa zea* (De Moraes et al. 1998). Tobacco, cotton and maize plants each release distinct blends of HIPVs in response to damage by these two herbivore species, and the wasp uses such blends as information to find their prey. When the attraction by plants resulted in the decrease of damage caused by the currently infesting herbivores, the attraction is called indirect defense of plants against herbivores. Herbivores also use HIPVs and undamaged plant volatiles for finding their host-food plants (Takabayashi 2014; Yoneya and Takabayashi 2013 for reviews).

Plant–plant communication and plant direct defense

Undamaged plants that have been exposed to HIPVs or to volatiles from artificially damaged plants become more defensive against herbivores than plants exposed to volatiles from undamaged plants (Arimura et al. 2009 for review) (Figure 1). This phenomenon is called “plant–plant communication.” Arimura et al. (2000a) showed that, under laboratory conditions, when exposed to HIPVs from lima beans leaves infested by two-spotted spider mites (*Tetranychus urticae*), the expressions of several defensive genes in exposed uninfested conspecific leaves were induced, and the exposed leaves were more defensive against the spider mites. Karban et al. (2006) showed that, under field conditions, sagebrush *Artemisia tridentate* exposed to volatile from artificially damaged

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Abbreviations: HIPVs, herbivore-induced plant volatiles; EFN, extrafloral nectar; JA, Jasmonic acid; SA, salicylic acid; PR, pathogenesis-related protein; LOX, lipoxygenase; PAL, phenylalanine ammonia-lyase; FRS, phanesyl pyrophosphate synthetase; CHS, chalcone synthaes; COMT, caffeic acid-*O*-methyltransferase; DGK1, diacylglycerol kinase 1.

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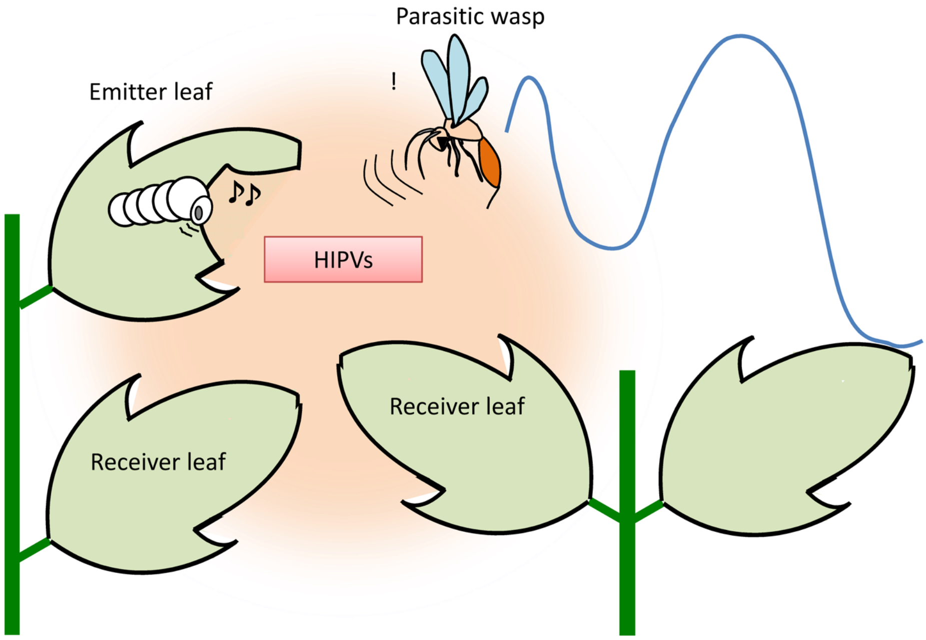

Figure 1. When infested by herbivorous arthropods, plants start emitting herbivore-induced plant volatiles (HIPVs). One of the well-known functions of HIPVs is to attract carnivorous natural enemies of herbivores. In this figure, a parasitic wasp is attracted by HIPVs from a leaf infested by herbivores. Once HIPVs are emitted, the infested plant can not control the use of the HIPVs. When a leaf of the same plant or a neighboring plant receives the HIPVs, the exposed leaf becomes more defensive against herbivory or pathogen infections. When the receiver is a neighboring plant, we call this plant–plant communication.

conspecifics suffered less herbivore damage when compared with unexposed conspecifics. They reported that volatiles from sagebrush plants infested by *Trirhabda pilosa* beetle had the same effect (Shiojiri and Karban, 2008a). Recently, Pearse et al. (2013) showed similar communication between intact and artificially damaged willow trees in the field. Currently, 48 well-replicated studies show plant–plant communications (Karban et al. 2014).

Plant–plant communication and plant indirect defense

By using cotton and lima bean plants, Bruin et al. (1992) and Dicke et al. (1990) showed that uninfested plants exposed to *T. urticae*-infested-plant volatiles attracted more predatory mites *Phytoseiulus persimilis* than uninfested conspecific plants exposed to volatiles from uninfested conspecific plants. An open question is whether this attraction is due to the active production of the attractive compounds (active response), or the absorption ofHIPVs on the surface of leaves and subsequent reemission (passive process) in the downwind plant. Choh et al. (2004) reported that uninfested lima bean plants exposed to volatiles from conspecific plants infested by *T. urticae* emitted a very similar blend of volatiles to that from the infested plants. Further, lima bean plants pre-treated with a protein-synthesis inhibitor prior to the exposure emitted the same blend of volatiles (Choh et al. 2004). These evidences support the hypothesis that the exposed lima bean plants absorbed HIPVs on their surface and re-emitted them (passive process). Interestingly, the exposed plants primed the production of HIPVs (see section *Priming*). Farag and Pare (2002) reported that, after exogenous application of (*E*)-2-hexenal to uninfested tomato plants, an increase in the release of local and systemic herbivore-induced monoterpenes and sesquiterpenes was observed, indicating an active response. Likewise, Engelberth et al. (2004) reported that (*Z*)-3-hexenyl acetate induced intact undamaged corn seedlings to produce jasmonic acid and emit sesquiterpenes. Under field conditions, Kost and Heil (2006) showed that lima bean tendrils infested by several herbivore species emitted volatiles, and such volatiles induced the production of extrafloral nectar (EFN), which is one of the indirect defense strategies in lima bean plants, in conspecific plant neighbors.

Plants recognize herbivores on their neighbors

An intriguing question is whether plants respond differently to volatiles from plants infested by herbivores that pose greater or lesser degrees of danger. Choh et al. (2013) examined EFN secretion in lima bean plants exposed to volatiles from cabbage plants infested by common cutworms (*Spodoptera litura*), two-spotted spider mites, or diamondback moth (*Plutella xylostella*) larvae. The first two herbivore species feed on lima bean plants but diamondback moth larvae do not. Only when exposed to volatiles from cabbage plants infested by spider mites, lima bean plants significantly increased their EFN secretion compared with plants exposed to uninfested cabbage volatiles. Of the three herbivore species, spider mites were the most likely to move from cabbage plants to lima bean plants and thus presumably posed the greatest threat, suggesting that plants may tune their defense levels according to the level of herbivore risk. Although chemical analyses showed herbivore-species-dependent differences in the volatiles produced by herbivore-infested cabbage plants, which compounds or blends triggered the increased secretion of EFN by lima bean plants remains unclear.

Plant–plant communications and herbivore performance

To date, studies on plant–plant communication have focused on defensive responses of plants. By contrast, effects of such a defensive phenomenon on performances of herbivorous insects have not been clearly shown. Recently, Yoneya et al. (2014) reported a study in which uninfested willow (*Salix eriocarpa*) plants were placed downwind of willow plants infested by larvae of willow leaf beetle *Plagiodera versicolora* for 4 days in a wind tunnel. After exposure, downwind plants were challenged by leaf beetle larvae. Pupal weight, larval survival rates, and leaf area consumed by larvae all decreased significantly, and duration of larval development increased significantly, on willow plants downwind of infested-plants compared to plants downwind of uninfested plants. These results showed that airborne information from infested willow plants negatively affected the performances of leaf beetle larvae.

Kin selection in plant–plant communication

In plant–plant communication, it has been thought that benefit goes to the volatile-receiver plants but not to the volatile-emitter plants. Thus, plant–plant communication is sometimes called "eavesdropping plants." However, there is a case in which kin selection is involved in plant–plant communication. Karban and his co-workers suggested that plant–plant communication results in kin selection in sagebrush under field conditions (Karban et al. 2013). Sagebrush propagates clonally belowground, and daughter ramets grow near the mother stem. Artificially damaged leaf volatiles of sagebrushes varied among genetically different ramets, although clonal ramets released similar volatiles, suggesting a genetic basis for volatile similarity (Ishizaki et al. 2012). Plant–plant communication in sagebrush was more effective among sagebrushes that were more closely related, indicating that plants responded differently to volatile cues from kin, making it more likely that receivers would respond to cues from relatives (Karban et al. 2013).

Communication within plants

Plant–plant communications may be the consequences of systemic responses within an individual plant against biotic stress without using vascular connections (Heil and Karban, 2010) (Figure 1). In fact, in some plants, there are potential vascular constraints on connection between branches (Frost et al. 2007; Heil and Silva Bueno 2007; Karban et al. 2006). Heil and Silva Bueno (2007) studied this in lima bean plants at their natural growth site by focusing on EFN secretion that attracts predatory arthropods and represents an induced defense mechanism. When exposed to HIPVs of neighboring plants or of the same shoot, EFN secretion by receiver leaves increased. They discussed the function of HIPVs as external signals for within-plant communication. Shiojiri and Karban (2008b) reported that, in a sagebrush, communication between damaged and undamaged stems required volatiles. These data suggest that volatile communication among plant stems or individuals may not be an unusual phenomenon.

Future directions

To date, induced defense responses in receiver plants that influence the behavior and performance of herbivorous and carnivorous arthropods have been focusing on the individual level. However, it remains under-explored how plant–plant communication affects the properties at population and community levels (e.g., population stability and species coexistence). It is important to note that, once volatiles have been emitted, plants cannot control their use. It would be interesting to study the consequences of information transfer to unintended organisms, such as to other competitive plant individuals, parasitic plants, etc. (e.g. Runyon et al. 2006). Such exploitative uses would be ecological costs (e.g. Strauss et al. 2002). Furthermore, a mathematical modeling study predicted that plant–plant communication between conspecific individuals might be regarded as a beneficial cooperative strategy rather than an eavesdropping strategy (Kobayashi and Yamamura 2007). One of the future research directions will be to understand the possible diverse roles of plant–plant communication in complex ecological networks.

Plant physiology of plant–plant communication

Specific response to volatile compound species

Arimura et al. (2000a) reported that the expression of jasmonic acid (JA)-responsive genes [*basic pathogenesis-related protein 2* (*PR-2*), *basic PR-3, lipoxygenase* (*LOX*), *phenylalanine ammonia-lyase* (*PAL*) and *farnesyl pyrophosphate synthetase* (*FRS*)] was induced in uninfested lima bean leaves in response to HIPVs from conspecific leaves infested by two-spoted spider mites in a glass container. They also showed these responses using potted lima bean plants (Arimura et al. 2001).

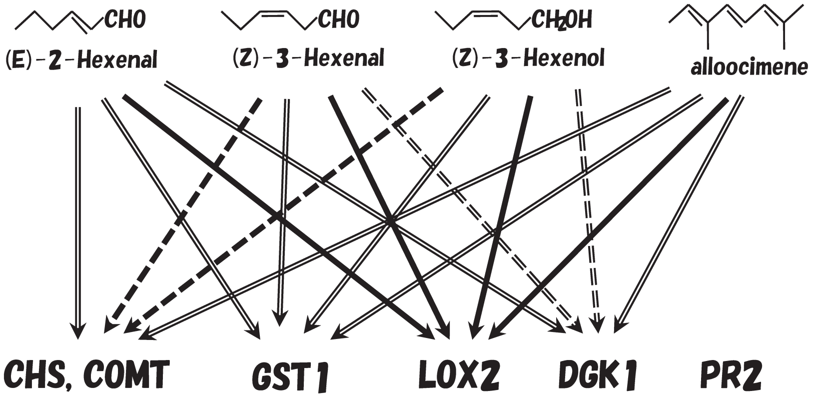

Figure 2. When Arabidopsis is exposed to either (*E*)-2-hexenal, (*Z*)-3-hexenal, (*Z*)-3-hexenol or *allo*-ocimene (2,6-dimethyl-2,4,6-octatriene), the expressions of *chalcone synthaes* (CHS), *caffeic acid-O-methyltransferase* (COMT), *glutathione-S-transferase1* (GST1), *lipoxygenase2* (LOX2) and *diacylglycerol kinase1* (DGK1) are induced in different manners. The expression of *pathogenesisrelated protein 2* (PR2) is not affected by the volatiles. Dotted lines indicate weaker induction than the solid lines. Open lines indicate that the induction was suppressed in *jar1* mutant. These data suggest that Arabidopsis responds differently to different volatile compounds that are structurally similar.

When uninfested lima bean leaves were exposed to each of the major HIPVs ((*E*)-*β*-ocimene, (*E*)-4,8-dimethyl-1,3,7-nonatriene, (*E*,*E*)-4,8,12-trimethyl-1,3,7,11-tridecatetraene), the compounds induced five JA-responsive genes with some differences of the time required until the detection of the inductions. Interestingly, one of the major HIPVs, linalool, did not induce the genes. Their data show that lima bean plants respond to different volatile compounds in different manner.

Heil et al. (2008) exposed lima bean plants to (*Z*)-3-hexenyl acetate, a substance naturally released from damaged lima bean and known to induce EFN secretion, and structurally related compounds, (*E*)-3-hexenyl acetate, (*E*)-2-hexenyl acetate, 5-hexenyl acetate, (*Z*)-3-hexenylisovalerate, and (*Z*)-3-hexenylbutyrate. They all elicited significant increases in EFN secretion, demonstrating that neither the (*Z*)-configuration nor the position of the double-bond nor the size of the acid moiety is critical for the EFN-inducing effect.

Bate and Rothstein (1998) and Kishimoto et al. (2005) studied the effects of synthetic volatile compounds on Arabidopsis (note that the amounts of volatile compounds used were higher than those detected from artificially damaged Arabidopsis). Kishimoto et al. (2005) monitored the expression profiles of the genes involved in defense responses upon exposing Arabidopsis to volatiles [(*E*)-2-hexenal (*α*,*β*-unsaturated ketone), (*Z*)-3-hexenal (*β*,*γ*-unsaturated ketone), (*Z*)-3-hexenol and *allo*-ocimene (2,6-dimethyl-2,4,6-octatriene)] (Figure 2). Genes known to be induced by mechanical wounding and jasmonate application [*chalcone synthase* (*CHS*), *diacylglycerol kinase1* (*DGK1*), *caffeic acid-O-methyltransferase* (*COMT*), *glutathione-S-transferase1* (*GST*) and *LOX2*] were shown to be induced with these volatiles. Chemically inert compounds, (Z)-3-hexenol and *allo*-ocimene, were also potent, suggesting that chemical reactivity was not the sole requisite for the inducing activity. With a jasmonate-insensitive mutant (*jar1*), the induction by the volatiles was mostly suppressed, however, that of *LOX2* was unaltered (Figure 2). In addition, a salicylic acid-responsive gene, *PR2*, was not induced by the volatiles (Figure 2). A protein phosphatase inhibitor, okadaic acid, efficiently suppressed the induction of defense genes in Arabidopsis by the volatiles [(*E*)-2-hexenal, (*Z*)-3-hexenal, (*Z*)-3-hexenol and *allo*-ocimene]. These data suggested that protein dephosphorylation is involved in the induction of the defense genes by the volatile compounds (Kishimoto et al. 2005). In corn plants, (*Z*)-3-hexenal, (*Z*)-3-hexenol, and (*Z*)-3-hexenyl acetate have nearly identical priming activity (Engelberth et al. 2004).

Response of plants to the volatile compounds with stereochemical differences

Whether plants respond differently to stereochemical differences of volatile compounds is an intriguing question. Root growth of Arabidopsis seedlings on the surface of agar plates was measured after the seedlings were exposed to volatile organic compounds (+)-bornyl acetate, (−)-bornyl acetate, (+)-borneol, (−)-borneol, or methanol (control) (Horiuchi et al. 2007). Seedlings with exposure to bornyl acetate exhibited wavy roots. Roots from seedlings exposed to (+)-bornyl acetate were significantly longer than those from seedlings exposed to (−)-bornyl acetate. Likewise, the roots from seedlings treated with (+)-borneol were significantly longer than those from seedlings exposed to (−)-borneol. In addition, when exposed to either (−)- or (+)-borneol, the seedlings did not show the wavy roots, but showed specific morphology, i.e. thick root tips, an increased number of root hairs and expanded root cells. These data suggested that the Arabidopsis seedlings specifically responded to stereochemical differences of volatile compounds.

Blends rather than a single compound, mediate plant–plant communication

Kikuta et al. (2011) reported an interaction between artificially damaged *Chrysanthemum cinerariaefolium* (insect flower) seedlings and undamaged conspecific seedlings. When intact seedlings were placed next to damaged seedlings, production of pyrethrin was induced. They also found the same induction when intact seedlings were exposed to a synthetic mixture of volatiles from artificially damaged leaves, i.e. (*Z*)-3-hexenal, (*E*)-2-hexenal, (*Z*)-3-hexen-1-ol, (*Z*)-3-hexenyl acetate and (*E*)-*β*-farnesene. Interestingly, however, when uninfested seedlings were exposed to the compounds separately, the induction was not detected, indicating that the volatiles from artificially damaged leaves function as a blend to control the biosynthesis of secondary metabolites. Under field conditions, Karban and his co-workers found evidence suggesting the importance of blends in plant–plant communication in sagebrush *Artemisia tridentate* (see Kin selection in plant–plant communication).

Signaling pathway involved

Arimura et al. (2000a, 2001) reported that JA-responsive genes were induced in response to HIPVs, but a salicylic acid (SA)-responsive gene, *acidic PR 4*, was not induced by the volatiles, suggesting that the JA signaling pathway is involved in plant–plant communication in lima bean plants, but the SA signaling pathway is not. Arimura et al. (2000a) further showed that the signaling pathway(s) mediating expression of defense genes in lima bean receiver leaves would include the calcium influx into cells, protein phosphorylation and dephosphorylation steps. Arimura et al. (2002) discussed that, in lima bean leaves exposed to *T. urticae*-induced volatiles, ethylene biosynthesis might be regulated by pathways involving JA and the ethylene positive feedback loop. Engelberth et al. (2007) reported that the octadecanoid signaling pathway in corn was affected by (*Z*)-3-hexenyl acetate, and the effects were not identical to those induced by insect elicitors.

In *jar1* of Arabidopsis, the induction by the volatiles [(*E*)-2-hexenal, (*Z*)-3-hexenal, (*Z*)-3-hexenol and *allo*-ocimene] was suppressed, except for *lipoxygenase2*, suggesting that both JA-dependent and -independent pathways were involved in the perception of the volatiles (Kishimoto et al. 2005). By focusing on accumulation of antifungal substances, and resistance against gray mold *Botrytis cinerea*, Kishimoto et al. (2006a) compared the responses of Arabidopsis mutants deficient in various signaling pathways; i.e., *etr1-1* (ethylene resistant), *jar1-1* (jasmonate resistant), *npr1-1* (salicylic acid insensitive), and *pad2-1* (phytoalexin-deficient) to (*E*)-2-hexenal and (*Z*)-3-hexenal with those of wild type (WT) plants. They suggested that ETR1-, JAR1-, and PAD2-dependent signaling pathways were involved in the response to C6-aldehyde-treatment. Among these, PAD2-dependent signaling appeared to be most important. In contrast, the involvement of NPR1-dependent signaling was minimal. Kishimoto et al. (2006b) studied the effects of a volatile monoterpene hydrocarbon, *allo*-ocimene, on the defense response of Arabidopsis against *B. cinerea* using *etr1-1, jar1-1, npr1-1* and wt. *allo*-Ocimene also enhanced resistant against *B. cinerea* in either wt, *etr1-1, jar1-1 or npr1-1*, suggesting that a signaling pathway independent of ETR1, JAR1 and NPR1 was operative in the resistance induced by *allo*-ocimene.

Priming

When infested by *T. urticae*, HIPVs-exposed uninfested lima bean leaves emitted more HIPVs than control leaves (leaves exposed to uninfested leaf volatiles), supporting the hypothesis that the HIPVs-exposed uninfested plant is primed for the production of HIPVs (Choh et al. 2004). Engelberth et al. (2004) reported that corn seedlings previously exposed to green leaf volatiles (GLV) from neighboring plants produced significantly more jasmonic acid and volatile sesquiterpenes when mechanically damaged and subsequently treated with caterpillar regurgitant application than seedlings not exposed to GLV. Further, cabbage, corn, hybrid poplar and hybrid aspen are reported to show priming responses when exposed to HIPVs (Frost et al. 2007, 2008; Li et al. 2012; Peng et al. 2011; Ton et al. 2007). Interspecific priming between artificially damaged sagebrush (*Artemisia tridentata*) and undamaged wild tobacco (*Nicotiana attenuata*), under both laboratory and field conditions has also been reported (Kessler et al. 2006).

How sensitive plant–plant communication can be

A crucial question is how far plant–plant signals can travel, given the dilution of airborne chemicals over a distance. Field studies showed that the effective distances in plant–plant communication in lima bean plants and sagebrush were ca. 50–60 cm (Heil and Adame-Álvarez 2010; Karban et al. 2006). By contrast, the data of Dolch and Tscharntke (2000) and Tscharntke et al. (2001) suggested that the distance was as great as 10 m or more (note that cues in their studies were either airborne or soil-borne). One can rephrase the above question as "how sensitive is the receiver plant to the volatile concentration" (Giron-Calva et al. 2012; Shiojiri et al. 2012). Shiojiri et al. (2012) showed that intermittent exposure over 3 weeks to trace amounts (ca. 140 pptV) of green leaf volatiles emitted by a freshly damaged *Arabidopsis* plant induced physiological (defensive) responses in undamaged neighboring plants. This demonstrates that in the long run, repeated exposure makes plants respond to subcritical amounts of chemical signals, and that plant–plant signaling may be as sensitive as olfactory signaling in animals.

How do plants receive volatiles?

As mentioned above, plants show specific responses to different volatile compounds or the same compounds with different congfigurations, suggesting the presence of specific volatile-receiving systems. However, to date, how plants receive volatiles is largely unknown. Zebelo et al. (2012) studied early events in plant–plant communication in tomato by focusing on plasma membrane potential (V-m) variations and cytosolic calcium ($[Ca^{2+}]$(cyt)) fluxes. Receiver tomato plants respond within seconds to herbivore-induced volatiles with a strong V-m depolarization, and V-m depolarization is found to increase with increasing concentration of green leaf volatiles. GLVs were also found to induce a strong $[Ca^{2+}]$(cyt) increase, particularly when (*Z*)-3-hexenyl acetate was tested both in solution and as a gas.

Sugimoto et al. (2014) found that undamaged tomato plants exposed to volatiles emitted by conspecifics infested with common cutworms (exposed plants) became more defensive against the larvae than those exposed to volatiles from uninfested conspecifics (control plants) in a wind tunnel. Comprehensive metabolite analyses showed that only the amount of (*Z*)-3-hexenyl-vicianoside (HexVic) was higher in exposed than in control plants. This compound negatively affected the performance of common cutworms when added to an artificial diet. The aglycon of HexVic, (*Z*)-3-hexenol, was obtained from neighboring infested plants via the air. The specific reception of airborne (*Z*)-3-hexenol to form HexVic in undamaged tomato plants reveals a previously unidentified mechanism of plant defense. Further, Sugimoto et al. (2015) reported that the exposure of Arabidopsis to a variety of different volatile alcohols including (*Z*)-2-pentenol, (*Z*)-3-hexenol, (*Z*)-3-heptenol, (*Z*)-3-octenol and (*Z*)-3-nonenol led to the accumulation of the corresponding glucosides. The exposure of the plants to cyclohexanol, benzyl alcohol, verbenol, perillyl alcohol, myrtenol, geraniol, or linalool also led to the detection of the corresponding glucosides (Sugimoto et al. 2015). These data shows a novel mechanism to receive a volatile alcohols in plant–plant signaling.

Kishimoto et al. (2006a) reported that PAD2-dependent signaling appeared to be most important when Arabisopsis was exposed to (*E*)-2-hexenal and (*Z*)-3-hexenal, respectively. Arabidopsis *pad2-1* muntant lacks γ-glutamylcysteube synthetase, which catalyzes the first step in glutathione biosynthesis (Parisy et al. 2007). In Arabidopsis, (*E*)-2-hexenal treatment resulted in the prodution of (*E*)-2-hexenal-glutathione adduct (Davoine 2006, Mirabella et al. 2008). Thus, it is likely that the airborne (*E*)-2-hexenal and other volatile aldehydes were taken in by the exposed plants to form aldehyde-glutathione adduct. If so, gluathione is one of the volatile-receiving molecules in addition to the above-mentioned glycosylation process.

Future directions

In plant–plant communication, volatiles (HIPVs or artificially damaged plant volatiles) induce defense-related genes, signaling pathways, and secondary metabolites in receiver plants that render them more defensive against biotic stress. Herbivory and exposure to volatiles may differentially induce the diefense responses in plants (e.g. Engelberth et al. 2007). Further, the modes of defense actions differ according to the chemical structure of the volatile compounds and blend composition. To clarify such differences, transcriptome analyses (Arimura et al. 2000b; Engelberth et al. 2013) and metabolome analyses (Sugimoto et al. 2014) would be needed. Engelberth et al. (2013) studied the effects of (*Z*)-3-hexenol on corn plants with microarray analyses. They showed novel information about the complexity of (*Z*)-3-hexenol induced transcriptional networks. Further, the effects of a blend of plural volatile compounds would be different from those of a single compound (e.g. Kikuta et al. 2011). Thus, the comparative plant physiological studies on plant–plant communications using several synthetic volatile compounds would be needed. Further, an intriguing question is how plants receive volatile compounds. It is unlikely that plants have the same odorant receptors as animals have (unpublished data). To date, the mechanism to receive a volatile chemical (*Z*)-3-hexenol in plant–plant signaling is merely reported (Sugimoto et al. 2014). This would be a tip of iceberg of the volatile sensing by plants. How plants receive to diverse volatile compounds should be addressed.

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