Emerging complexity: jasmonate-induced volatiles affect parasitoid choice

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Plant responses to specific environmental stimuli at the molecular and genetic levels have been widely reported in recent decades, mainly as a consequence of the availability of new laboratory techniques. However, understanding the complex implications of these observations at the ecosystem level remains one of the greatest challenges facing plant science today. Recently, new experimental strategies have been designed to address complex interactions. For example, combinations of different insects have been used to study insect–plant interactions (Dicke et al., 2009) as well as parallel analysis of the responses to different types of pathogen which reflect more closely the conditions encountered in natural ecosystems (Pieterse et al., 2009).

In this issue, the two papers by Bruinsma and colleagues also address such complex issues; the detailed analysis of plant responses to different herbivores and JA application are documented, and the responses of parasitic wasps that attack the herbivores are recorded. The authors’ experimental design and interpretation of the results highlight the importance of understanding the complexity of plant responses in the context of a whole ecosystem.

In the last two decades, interest in plant–insect interactions using ecological, chemical, and molecular approaches has increased dramatically. Direct defence reactions of plants, such as the production of toxins or deterrent proteins like proteinase inhibitors, as well as indirect defence reactions, have been identified showing that the effectiveness of the natural enemies of attackers can be altered. In the latter case, the induced release of volatiles is a common phenomenon leading to the attraction of carnivores. Plants attacked by herbivores respond with the establishment of a chemical phenotype, releasing volatiles into the atmosphere that include terpenoids, phenylpropa- noids or fatty acid-derived green leaf volatiles. The detailed composition of the volatile blend is insect-specific and depends on the type of attacker (e.g. chewing or sucking insects) and on their oral secretions released at the wound site of the plant. Moreover, the plant responses are different depending on whether the organs under attack are above or below ground. One basic question when analysing plant responses is what underlying mechanism leads to the expression of genes encoding the enzymes in volatile biosynthesis and the formation of deterrent proteins. A well-known signalling compound active in plant responses to wounding by herbivores, such as caterpillars, is jasmonic acid (JA) (Kessler and Baldwin, 2002). JA is known to regulate many plant responses to biotic and abiotic stresses and is active in the regulation of plant development (Wasternack, 2007). The challenge of present day studies is in understanding a plant’s responses to multiple attackers, for example, by analysing the responses in terms of volatile production and/or the attraction of parasitoids in a double-attacker (e.g. above- and below ground) context (Dicke et al., 2009; Poelman et al., 2008).

The papers by Bruinsma et al. (2009a, b), founded on the long-term experience of the senior author’s laboratory in the analysis of tritrophic interactions, demonstrate a role for herbivore-induced plant volatiles in the attraction of the natural enemies of those herbivores. As a model plant, Brussels sprout, Brassica oleracea L. var. gemmifera, was used. Caterpillar-infested Brussels sprout plants attracted parasitoids such as Diadegma semiclausum and several Cotesia spp. within one hour of infestation. The experimental design was established with three species of parasitoids, Cotesia rubecula, C. glomerata, and D. semiclausum, which differ in their host range and specificity. Hosts of these parasitoids are Pieris sp. (cabbage white butterfly) or Plutella xylostella (diamondback moth) caterpillars, respectively. The aim of the work was to determine the preference of parasitoids for volatiles from JA-treated, herbivore-infested or control plants in terms of time, dose effects, volatile blend, and levels of JA and its precursor 12-oxophytodienoic acid (OPDA). Interestingly, in a comparison with untreated plants, the three parasitoids preferred plants emitting volatiles induced by JA-treatment, but, in the case of specific choice experiments between the JA-treated plants and herbivore-infested plants, they preferred the latter. This preference was time- and dose-dependent (Bruinsma et al., 2009b). As expected, herbivore attack led to an increase in JA levels. However, this increase was not accompanied by a concomitant increase in OPDA levels after Plutella xylostella attack, whereas attack by Pieris rapae (small cabbage white) increased the levels of both compounds. This is intriguing and of specific importance for the composition of the volatile blend. There are an

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increasing number of examples for specific responses mediated by JA and OPDA, for example, different sets of genes are expressed in response to JA or to OPDA (Taki et al., 2005; Mueller et al., 2008). The most convincing result in this respect is the establishment of resistance in JA-deficient Arabidopsis thaliana mutant plants, which were affected in the JA biosynthesis downstream of OPDA indicating that OPDA can mediate defence reactions (Stintzi et al., 2001).

In their response to different herbivores, plants are able differentially to generate various oxylipins, such as JA and OPDA. In the light of recent mechanistic interpretation on JA signalling, the question arose: How does independent perception of JA and OPDA take place? Many JA-induced genes are expressed by the action of the transcription factor MYC2, but, under non-induced conditions, this factor is negatively regulated by the so-called JAZ (Jasmonate ZIM domain) proteins (Chico et al., 2008; Katsir et al., 2008; Staswick, 2008). JAZ proteins are subjected to proteasomal degradation after interaction with the F-box protein COI1. This interaction, however, takes place only if the JA–isoleucine conjugate is present. Amino acid conjugates of JA are formed by the JA-conjugate synthetase from JA and an amino acid, such as isoleucine (Staswick, 2008). More precisely, only a distinct enantiomer, the (+)-7-iso-jasmonoyl-L-isoleucine, exhibits high bioactivity in mediating JAZ–COI1 interaction (Fonseca et al., 2009). Consequently, the window of time for JA-responsive gene expression is determined by the generation and epimerization of a JA-related compound and by the occurrence and stability of the JAZ proteins. However, so far, none of the 12 JAZ proteins of Arabidopsis thaliana accept OPDA as a ligand in the interaction with COI1 (Browse, 2009). It is still not known how OPDA, generated in a plant after herbivore attack as described above, is perceived and transduced leading to a specific blend of volatiles. However, such specificity with respect to signalling compounds is nicely documented by Bruinsma et al. (2009b) for the first time in a plant of agricultural importance.

The crucial question in the work of Bruinsma et al. (2009a, b) is the link between herbivores, parasitoids, oxylipins, ion-channel-forming peptides such as alamethicin (ALA), and the composition of the volatile blend. Fifty-three compounds were identified among the volatiles including terpenoids, ketones, alcohols, aldehydes, nitriles, sulphides, and esters. Among them (Z)-3-hexenyl-1-yl acetate, limonene, β-myrcene, and α-thujene exhibited the highest levels. Statistical and principal component analyses allowed a comparison of the different treatments. As stated earlier, in the choice experiment between JA-treated plants and herbivore-infested plants, parasitoids preferred the latter group, indicating that they can discriminate between artificial and herbivore induction. Obviously, in the herbivore induction there are more factors than JA involved, which is consistent with many recent studies (cf. Dicke et al., 2009). This aspect was specifically addressed in Bruinsma et al. (2009a) by the analysis of volatile emissions and parasitoid attraction upon JA and/or ALA treatment. ALA is a peptide mixture formed by the fungus Trichoderma viride and is known to form voltage-gated ion channels (Engelberth et al., 2000). Oral secretions of cabbage white butterfly larvae form ion channels in artificial membranes, suggesting the occurrence of ion channel-forming compounds in such oral secretions. Consequently, Bruinsma et al. (2009a) used ALA to manipulate an early step (alterations of membrane potential, Ca2+ signalling) in the signal transduction of induced plant defence. ALA was found to act upstream of JA and both compounds led to the formation of distinct volatile blends. Most importantly, ALA-treated plants were much more attractive to C. glomerata than JA-treated plants (20-times, if calculated on a molar basis of the compounds used). This indicates that, within an induced defence signal transduction occurring in tritrophic interaction, different steps act to a different degree, which may have an evolutionary impact.

Interestingly, the Brussels sprout plants showed great differences in the degree of volatile emission and caterpillar infestation rate compared to A. thaliana, supporting the significance of the work done by Bruinsma and co-workers in concentrating on a crop plant. The importance of using agriculturally important plant species and cultivars is also indicated by the recently observed cultivar-specific differences of four B. oleracea cultivars in the interaction with the aphid Brevicoryne brassicae (Broekgaarden et al., 2008). The data concerning Brussels sprouts demonstrated the role of both the quantitative and the qualitative composition of the volatile blend. Interestingly, wasps were more attracted by plants with a lower overall quantity of volatiles as a result of herbivore infestation than by the higher quantities released after treatment with JA. However, JA-treated plants were attractive for much longer. As well as the role of the right time window, the role of sensitivity within this tritrophic interaction was shown to be an important parameter: the wasps could distinguish plants without treatment (control) and with treatments using low concentrations of JA (10 μM), by preferring JA-treated plants. By contrast, the herbivore Pieris rapae could not distinguish between control plants and plants treated with 10 μM JA, although it preferred control plants over plants treated with high JA concentrations (Bruinsma et al., 2007). This indicates a higher sensitivity of the parasitoids when compared with the herbivores.

The papers of Bruinsma et al. (2009a, b) and related papers on herbivory and JA signalling suggest several parameters which influence the outcome of a tritrophic interaction, thus being of interest in crop improvement in the natural environment: (i) cultivar specificity of herbivores; (ii) specificity and sensitivity of parasitoids; (iii) timing and strength of the plant response upon herbivore infestation; (iv) synthesis and perception of specific signalling compounds, such as ion channel-forming compounds or the oxylipins OPDA and JA; (v) different degree of responses in early and late steps of signal transduction; (vi) expression, half-life, and specificity of JAZ proteins; (vii) quantity and composition of the volatile blend; and (viii) specificity of volatiles in affecting oviposition.
There is an increasing body of evidence demonstrating that the co-evolution of plants, herbivores and parasitoids increases the complexity of tritrophic interactions. Examples of inputs to these systems include a network of plant signalling compounds (hormones, such as ethylene and salicylic acid; Pieterse and Dicke, 2007; Poelman et al., 2008; Pieterse et al., 2009) and the selection pressure imposed by associative learning (such as in sexual communication system of parasitic wasps; Huigens et al., 2009). Careful observation and documentation of inputs and responses, combined with the functional interpretation of underlying scenarios, will lead to a better understanding of the nature of tritrophic systems. Furthermore, the rapidly growing methodological potential provided by genomic, transcriptomic, proteomic, and metabolomic approaches, combined with bioinformatics, will provide essential information to inform the design of biotechnological and field applications.

References


