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EDITED AND REVIEWED BY Stefano Colazza, University of Palermo, Italy

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RECEIVED 16 July 2023 ACCEPTED 21 July 2023 PUBLISHED 04 August 2023

CITATION

Wink M and Legal L (2023) Editorial: Chemical ecology of plant arthropod interactions: how do herbivorous arthropods cope with defence chemicals of their host plants? *Front. Ecol. Evol.* 11:1259549. doi: 10.3389/fevo.2023.1259549

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Editorial: Chemical ecology of plant arthropod interactions: how do herbivorous arthropods cope with defence chemicals of their host plants?

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KEYWORDS

secondary metabolites, sequestration, tolerance, acquired defence, plant-insect interactions, defence chemicals

Editorial on the Research Topic

Chemical ecology of plant arthropod interactions: how do herbivorous arthropods cope with defence chemicals of their host plants?

Plants produce a high diversity of Secondary Metabolites (PSM) (or specialized metabolites; natural products) as defence compounds against herbivores and microbes. In addition, PSM can serve as signal compounds to attract pollinating insects and seed-dispersing frugivores. Despite plant chemical defence which evolved over 500 million years (Mallik and Inderjit, 2002; Wink, 2020), many arthropods are herbivorous. How do they cope with the defence chemistry of their host plants?

Many arthropods have powerful detoxification systems, which prevent the uptake or accumulation of toxins in the animal. Several arthropods have only one or a few host plants and thus are particularly adapted to the defence chemistry of their host plants (Blum, 1981; Meinwald, 2003; Bagnères and Hossaert-McKey, 2016; Wink, 2018; Wink, 2019). Adaptations can involve: 1. Tolerance to a toxin *via* modification of the molecular target to which the PSM was directed. 2. Detoxification and or rapid elimination of dietary PSM. 3. Active sequestration of a PSM and its utilisation as an acquired defence compound against predators. 4. In case, that toxic PSM are stored in insects, they often show aposematic colouration as a warning signal to potential predators.

We hoped to attract interesting manuscripts for the Research Topic titled "*Chemical Ecology of Plant Arthropod Interactions: How do Herbivorous Arthropods Cope with Defence Chemicals of Their Host Plants?*" Our Research Topic should cover various aspects of plant defence, plant–insect interactions and chemical ecology. This Research Topic includes 6 publications from international authors published in 2022 and 2023.

Plant response to herbivory

The article by Fiedler et al. focuses on a complex plant-insect relationship. Sphingidae and especially those of the genus *Hyles* (Lepidoptera) are known to be able to feed on highly toxic plants (Wink and Theile, 2002), as in the case of this study on *Euphorbia* rich in phorbol esters. This study shows that several chemically related products have variable distributions in plant tissues and different functions in the plant's defence strategy. Interestingly, only one of the phorbol esters present appears to be regulated quantitatively as a function of herbivory pressure, while the other two phorbol esters present appear to have distinct roles, demonstrating the complexity of plant-herbivore co-evolution.

Comparison of responses to anti-herbivory substances

Cardenolides are among the most effective compounds against herbivory, but some insect species have managed to develop complex mechanisms for feeding on plants containing this chemical family (Blum, 1981; Holzinger et al., 1992). In this article by Rubiano-Buitrago et al. the model heteropteran Oncopeltus fasciatus is tested against several cardenolides from Asclepias curassavica, an Asclepiadaceae whose chemical composition is best known. One of the original aspects of this work is to compare the response of the Na⁺/K⁺-ATPase pump of the insect adapted to this plant versus a non-adapted insect (Drosophila melanogaster) and also the enzymatic equivalent of a mammal (Sus domesticus). Depending on the products tested, some are more easily sequestered than others, but this involves an energy cost for the specialised insect. The concentration of product sequestered was curiously independent of the potential for inhibition of the Na⁺/K⁺-ATPase pump. This shows that there are still poorly understood synergistic aspects between these cardenolides. In addition, although the Drosophila model is very sensitive to the toxicity of these products, it remains much more tolerant to cardenolides than the mammalian model.

Co-evolution: How compounds that are repellent to herbivores are attractive to certain specialist insects

In many cases, the reason for studying a plant-insect relationship is to control a species which, because of its specialisation, is categorised as a plant pest in relation to the production of a plant of economic interest. This is the case of *Diorhabda tarsalis* (Coleoptera) in relation to Chinese licorice; *Glycyrrhiza uralensis*, an important plant in traditional Chinese pharmacopoeia. In the article by Chen et al., the importance of this legume is emphasised. In this case, the products attractive to the target insect are a mixture of simple C6 compounds (aldehydes and alcohols) widely distributed in plants. One of the surprises of this study is that these compounds are generally repellent to many arthropods, so there is the potential for economically viable control of *D. tarsalis* by emitting these attractants outside the plant cultivation site.

Parasitoids with variable temporal response spectra and fruit specificity as a function of chemistry and dipteran infestation of fruit

The oriental fruit fly, *Bactrocera dorsalis*, is a major pest of fruit and vegetables worldwide, and its populations can be controlled using parasitoid Hymenoptera such as *Fopius arisanus* and *Diachasmimorpha longicaudata*. The study by Miano et al. focuses on the chemical compounds governing the specificity of parasitism. For both parasitoid species, infected fruit (in this case mangoes) emit compounds that indicate to hymenopterans the presence of *B. dorsalis* infestation. It should be noted that, depending on the hymenoptera species, it is not exactly the same products that are attractive, and that attraction does not occur at the same time. This means that the two parasitoid species can control the pest at different times. Finally, the authors show that the volatile compounds emitted by two different varieties of mango have variable attractiveness in terms of chemical composition and time without and after infestation by the fruit fly.

Comparison of cocktails of chemical compounds to improve the effectiveness of a parasitoid

One of the main insects harmful to tea production is the aphid *Toxoptera aurantii*. Only parasitic wasps of the *Aphelinus* genus are partially effective in controlling this aphid. However, this effectiveness is limited by the low attractiveness of the target insect to the parasitoids. The study by Wu et al. tested cocktails based on odours emitted by the plant and/or the target insect under different conditions. A first cocktail based on plant volatiles and another based on chemical compounds emitted by the aphid seem to have some effectiveness but it is the combination of the two (called attractant 3) that significantly increases the attraction of parasitoids of the genus *Aphelinus* in tea plantations infected by *T. aurantii*. This strategy could represent a reasonable environmental alternative to pure treatment with synthetic insecticides.

Virus modifying the egg-laying behaviour of a whitefly on chilli

We know that the success of the infestation of certain plant viruses is directly linked to their density on the infested plant. Whiteflies (Aleurods) are virus vectors and are most often found in high densities on plants, often resulting in the death of the plant. To complete their complex cycle, the viruses from these insects need to be incorporated in a relatively healthy plant, so a relatively low whitefly density is preferable for the virus. The study by Yadav et al. clearly shows a reduction in the egg-laying density of whiteflies carrying the virus on chilli plants already heavily infected with it. We can therefore observe a change in the behaviour of whiteflies depending on whether they are vectors (preference for healthy plants) or non-vectors (preference for infected plants). To confirm their results, the authors used qPCR to show that the regulation of certain genes linked to odour-binding proteins was altered depending on whether or not whiteflies were vectors of the virus. The hypothesis is that it is the virus itself that induces these changes in gene expression and consequently the insect's behaviour.

In conclusion, the results published in this Research Topic highlight important aspects of chemical ecology and plant- insect interactions. We hope that our Research Topic will be of great interest to both the general public and the scientific community.

Author contributions

MW: Conceptualization, Writing – original draft, Writing – review & editing. LL: Conceptualization, Writing – original draft, Writing – review & editing.

Acknowledgments

We thank the authors of the papers and the reviewers who made this volume possible.

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MW declared that they were an editorial board member of Frontiers, at the time of submission. This had no impact on the peer review process and the final decision.

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