Chemical Ecology of Chrysomelid Interactions with Plants and Parasitoids

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Ecosystems consist of complex trophic relationships between plants, herbivores, and their natural enemies. To study and control these complex associations, we require a basic understanding of plant location and choice behaviors of herbivores and of the defense strategies of their host plants. Chrysomelid beetles are very suitable organisms to study such multitrophic interactions since they offer a great variety of relationships with their host plants that have evolved under different ecological conditions. I am performing comparative studies of different plant – leaf beetle – parasitoid systems that include the distribution of natural populations, the behavior, sensory ecology and communication of all species involved. The aim of my research is to gain new insights into mechanisms controlling these systems, and to offer new approaches that will lead to the development of new or improved strategies for biological control.

I work at the Department of Applied Zoology/Animal Ecology, Free University of Berlin, headed by Monika Hilker. Our research focuses on the chemical ecology of insects. Chrysomelids (Hilker & Meiners 1999) as well as insect egg deposition (Hilker & Meiners 2002a) play a major role in our studies. Information transfer between plants, herbivorous insects, predatory and parasitic insects is mediated by a plethora of chemical signals and cues, such as, e.g., plant volatiles or pheromones. Our major aim is to unravel this infochemical web in several multitrophic systems by studying the mechanisms and functions of chemical communication. The identification of infochemicals involved in multitrophic interactions, studies of their biological activities, and investigations of their biogenesis are our major tasks. We use chemical and molecular techniques as well as modern behavioral assays for our studies. Knowledge of the chemical ecology of multitrophic interactions may contribute to a better understanding of the evolution of a food web and lead to an optimal use of naturally occurring chemicals in crop and forest protection.

Chemical Ecology of Plant Defenses Induced by Chrysomelid Egg Deposition

Plants defend themselves directly or indirectly with the help of parasitoids or predators against herbivores. They attract natural enemies of the herbivores by the emission of specific plant volatiles. The larvae and adults of the elm leaf beetle, Xanthogaleruca luteola (Fig. 1), are major natural pests of the European field elm (Ulmus minor), and can occasionally defoliate whole trees (Fig. 2). Field elms respond to oviposition of these beetles by releasing novel blends of volatiles, which attract the elm leaf beetle egg parasitoid Oomyzus gallerucae, even in the absence of herbivory. This system has been well characterized ecologically (Meiners & Hilker 1997; 2000; 2003; Hilker & Meiners 2002b; 2006; Meiners et al. 2000; 2005) and is an entirely natural system that has not been disturbed in any way by agricultural selection pressures. An elicitor from the oviduct secretion that glues the eggs to the leaf triggers the release of volatiles in the field elm that specifically attracts O. gallerucae, prior to any herbivory having occurred. This volatile release exactly coincides with the time needed for the leaf beetles eggs to hatch, whereupon the tree ceases to be attractive to the egg parasitoids. In a project funded by the German Research Council “Induction of plant volatiles by insect egg deposition on elm, Ulmus minor: using molecular methods and genetic transformation to understand an ecological phenomenon” I investigate the defense mechanisms of the elm further in cooperation with Trevor Fenning (MPI Chemical Ecology, Jena). It is the intention of this project to dissect how this exceptionally interesting suite of responses in elms is initiated and regulated at the molecular – genetic level. The research objectives are to determine (1) the mode of volatile induction by eggs of X. luteola at the level of gene expression, (2) how U. campestris regulates the production of the induced volatiles, (3) which genes and biochemical pathways are associated with the volatiles involved in leaf beetle and parasitoid attraction. I study furthermore in the lab and in the field a) the function of certain terpenoids and the meaning of background odours for the orientation of the egg parasitoid, b) the temporal and spatial variability of induced defenses within and between trees, c) plant-mediated mechanisms of aggregation. The plasticity of induced responses in plants caused by herbivore oviposition can certainly influence the presence and distribution of herbivores and parasitoids. The leaf beetles themselves might employ volatiles emitted...
as part of indirect plant responses to herbivore attack to localize con specifics or to avoid competition. While the lab work is done in Berlin, the collection and the field work is performed in elm stands Southern France and Northern Spain.

**Figure 2. Adult elm leaf beetle.**

**Chemical and structural diversity of the vegetation:**  
**Influence on chrysomelids and their parasitoids**

Often neglected aspects of biodiversity are the chemical and structural diversity of the vegetation and their effect on multitrrophic interactions. Up to date most studies have concentrated on the influence of plant diversity on host-parasitoid interactions in general and did not separate the effects of chemical and physical features. Plant chemical diversity as well as plant structures have been shown singly to influence the choice of oviposition places by herbivores and the host finding of the parasitoids. The combined influence of both factors on the interaction between herbivorous insects and their parasitoids in the field, as well as their scale dependency is not known. Together with Elisabeth Obermaier (Department of Animal Ecology and Tropical Biology, University of Würzburg) I investigate the function of the chemical complexity of habitat odors and the vegetation structure for leaf beetle - parasitoid interactions.

Our model system is the tansy leaf beetle *Galeruca tanaceti* (L.), its egg parasitoid, *Oomyzus galerucivorus* (Hymenoptera: Eulophidae), and its food plants (e.g. yarrow, *Achillea millefolium* (Asteraceae)). The leaf beetle (Fig. 3) and its egg parasitoid are common on grasslands (Fig. 4) all over mid-Europe. The beetle is polyphagous and feeds on species of the families Asteraceae, Brassicaceae, Caryophyllaceae, Dipsacaceae, Liliaceae, Lamiaceae, Polygonaceae, and Solanaceae (Lühmann, 1939; Prevett, 1953; Obermaier & Zwölfer, 1999). In autumn, females of the tansy leaf beetle deposit their egg clutches on vertical structures within the herbaceous vegetation layer, mostly on grass and other non-host plants, where the egg clutches then hibernate (Meiners et al., 2006). The gravid females are unable to fly (but see Been 2005) and have to walk up the plant structures for oviposition. After hatching in April-May, the larvae have to find suitable host plants in the surrounding of the oviposition site where they feed for about three weeks until pupation (Obermaier & Zwölfer, 1999). After pupation, the adults can be found from early June onwards before they enter a reproductive diapause in mid-summer. The eulophid wasp *O. galerucivorus* parasitizes different *Galeruca* species (Sinacori & Mineo, 1993), however, its main host in Germany is the tansy leaf beetle. *O. galerucivorus* parasitizes the egg clutches of its host shortly after beetle oviposition in autumn. The parasitoid larvae hibernate in the host eggs and adults emerge next spring (Meiners et al., 2006). The 1.5 mm long egg parasitoids search at close range for host egg clutches by walking up and down vertical structures within the vegetation and using chemical contact cues from the host faeces (Meiners et al., 1997). Parasitism caused by *O. galerucivorus* is the most immediate mortality factor for the egg clutches of *G. tanaceti* and parasitism rates can reach up to 90% (Meiners et al. 2006).

**Plant chemical diversity**

In the field the tansy leaf beetles chose oviposition sites on the basis of food plant presence and quantity; furthermore plant species diversity influenced oviposition site selection (Randlkofer et al. 2007). *G. tanaceti* females laid their egg clutches preferentially in the immediate vicinity of their main food plants (*A. millefolium* and *C. jacea*), which were present more often and in higher densities in oviposition plots compared to control plots within the investigated natural grassland habitats. By ovipositing close to the host plants *G. tanaceti* ensures ready access to nutritional resources for hatching larvae, despite the fact that their eggs may also be more subject to parasitism, since the presence of the host plant *A. millefolium* enhanced the probability of egg parasitism by *O. galerucivorus*.

Odour blends originating from host plants, non-host plants and diverse plant mixtures influenced oviposition site selection of the leaf beetle (Randlkofer et al. 2007). Oviposition olfactometer tests clearly showed that the female beetles responded during oviposition to the volatiles released by the plants. *G. tanaceti* preferred the odours of a diverse plant species mixture for oviposition, which always included food plants when tested against the other plant species.
odours of grass plants, which they mostly use as an oviposition substrate.

We have shown that experienced female parasitoids are attracted to odours from *A. millefolium* (Randlkofer et al. 2007). Our results indicate that *O. galerucivorus* can exploit host plant volatiles for host location, although an enhanced plant odour complexity hampered the orientation of the specialised egg parasitoid. In olfactometer bioassays with the parasitoid neither naïve nor experienced egg parasitoids were attracted to odours of a leaf beetle host plant (*A. millefolium*) when offered simultaneously with odours of a non-host plant (*T. vulgaris*). In contrast, there was a significant attraction of experienced but not of naïve parasitoids to the pure host plant odour. These results suggest that the egg parasitoid does not respond to the volatile cues emitted from the host plant of its host when the diversity of the volatile blend is enhanced by adding a non-host plant species, at least if it has not experienced this odour blend before.

**Plant structural complexity**

Field studies on calcareous grasslands revealed that structurally complex vegetation has profound effects on the foraging success of *O. galerucivorus*. On a small spatial scale (*r = 0.1 m*) a reduced probability of egg parasitism could be explained by the parameters vegetation density and vegetation height (Meiners & Obermaier 2004; Obermaier et al. 2007). The number of egg clutches in areas with different grass stem density is directly proportional to the number of stems in these areas (a similar probability of an oviposition event per stem in high and low stem density areas); the number of egg clutches in areas with high stem densities is disproportionately higher than in low stem density areas. At three investigated grassland sites of all vegetation structure parameters only the factors stem density and vegetation height were significantly positively correlated with the presence of egg clutches. Oviposition height of the leaf beetle is not uniform, but changes with the structure of the habitat and during the season (Obermaier et al. 2006). Mean oviposition height per site (70 cm) was significantly higher than mean vegetation height (28 cm). Our results suggest that females try to oviposit as high as possible in the vegetation and on the plants selected. In accordance with this, the probability of egg parasitism and of winter egg clutch mortality significantly declined with increasing oviposition height.

We will continue this work in a Priority Programme of the German Research Council in three Biodiversity-Exploratories (http://www.biodiversity-exploratories.de/) in Germany and study the influence of land use intensity on a) the chemical complexity of habitat odors and b) the vegetation structure and their function for the leaf beetle- parasitoid interactions. Further research on leaf beetles will also include a comparison with other *Galeruca* species. Thus, overwintering egg masses of different *Galeruca* species are very welcome.

**Literature:**


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