

FE SPOTLIGHT

Caterpillar feeding impairs an indirect defence: costs or strategy?

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The secretion of extrafloral nectar (EFN) represents a widely distributed and efficient inducible anti-herbivore defence. Providing sweet rewards on their vegetative parts enables plants to attract ants and other predators as well as parasitoids, which generally benefits the host plant. As plants are smart, they can also eavesdrop on signals of danger that are emitted by their neighbours. For example, lima bean (*Phaseolus lunatus*) plants respond with higher EFN secretion rates to the exposure to volatile organic compounds (VOCs) from infested neighbours prior to herbivore attack (Heil & Silva Bueno 2007; Blande, Holopainen & Li 2010), a response that benefits plants in terms of decreased rates of herbivory under natural conditions (Heil & Silva Bueno 2007). In short, EFN secretion is a common inducible defensive response whose responsiveness to herbivore-induced VOCs ensures that plants can prepare themselves successfully for future attack.

In this issue, however, Li *et al.* (2012) question the general applicability of these statements. The authors studied the herbivore-induced VOCs release and EFN secretion by hybrid aspen (*Populus tremula* × *tremuloides*) after exposure to the headspace of damaged conspecific neighbours. The authors found a direct induction of EFN secretion: hybrid aspen ‘smells’ when a neighbouring plant is damaged and then starts to attract ants as a preparation for future threats. By contrast, the emission of VOCs was not directly induced by an exposure to VOCs, although the exposed plants were primed to release higher amounts of monoterpenes, homoterpenes and sesquiterpenes when consecutively being infested by caterpillars. All these observations make ecological sense, because VOCs represent only information, whereas EFN is a resource (Kessler & Heil 2011). That is, a plant that emits herbivore-induced VOCs without being infested would ‘lie’ and ‘cheat’ its defenders. By contrast, EFN represents a resource *per se* that can enhance the survival of multiple predators such as lacewings (Limburg & Rosenheim 2001), predatory mites (Van Rijn & Tanigoshi 1999; Gnanvossou *et al.* 2005), parasitic wasps (Röse, Lewis & Tumlinson 2006) and ants (Lach, Hobbs & Majer 2009; Wilder & Eubanks 2010). Therefore, a direct induction upon to herbivore-induced VOCs makes ecological sense for EFN, but not so for VOCs.

However, in contrast to what represents a convenient and generally accepted state of the art in the research on tritrophic interactions and plant–plant signalling, Li *et al.* (2012) also report that VOCs did not prime EFN secretion for stronger increase upon direct herbivore damage. By contrast, feeding by caterpillars of autumn moth (*Epirrita autumnata*) impaired, rather than induced, the secretion of EFN on mature leaves. This result was confirmed for three different poplar clones: intact leaves of infested plants secreted less EFN than intact leaves of un-infested plants, and directly damaged leaves exhibited even lower secretion rates. Why does poplar reduce EFN secretion in response to caterpillar feeding? Because we are commonly not as open as we should be to unexpected ideas, the authors present various explanations for their seemingly inconvenient observation. First, feeding caterpillars might directly damage the extrafloral nectaries. Second, the feeding might damage the photosynthetic tissue to a degree that limits the *de novo* synthesis of sugars for EFN production. Third, caterpillar feeding might induce defensive responses that compete with EFN for limited resources and fourth, the caterpillars might possess a mechanism to actively suppress EFN secretion.

Although these arguments are non-exclusive, options two and four are those that will make this article the basis for many future studies. The authors discuss that the caterpillar, as a generalist, is unlikely to possess a mechanism for active manipulation of host defence. Is this necessarily true? In fact, generalist herbivores would gain particularly significant selective benefits from suppressing general plant resistance responses. Whereas specialist herbivores can evolve strategies against the specific resistance traits of their host, generalists are unlikely to evolve specific enzymes that allow for the successful detoxification of the entire arsenal of secondary compounds that they face in their multiple host species. In fact, generalists can possess multiple or highly promiscuous detoxification enzymes (Li, Schuler & Berenbaum 2003; Li *et al.* 2004; Pauchet *et al.* 2008), but the synthesis of multiple enzymes comes at high metabolic costs, whereas promiscuous enzymes are usually less efficient than specialized ones in accelerating any of the catalysed reactions. By contrast, suppressing general plant signalling pathways can render plants much more susceptible. For example, many *Pseudomonas* strains inject

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coronatine, a mimic of jasmonic acid, which results in the suppression of salicylic acid-dependent resistance to biotrophic pathogens. Similarly, generalist insect herbivores and necrotrophic pathogens release hormones that suppress jasmonic acid-dependent defence responses (Pieterse & Dicke 2007). Such strategies mean that generalists can suppress hundreds of defence-related genes. The secretion of EFN depends on jasmonic acid signalling, and ants represent a threat against which efficient countermeasures are difficult to evolve. Thus, it appears tempting to speculate that *E. autumnata* possesses a general mechanism to suppress EFN secretion on any of its potential host plants, which would allow this caterpillar to enter an enemy-free space on multiple taxonomically unrelated hosts.

An argument against this idea is that both EFN and VOCs are induced via the same signalling pathway, and VOCs were primed for induced release after caterpillar feeding on aspen (Li *et al.* 2012). Although direct quantifications of metabolic costs are missing, we can reasonably assume that VOCs (usually released in micrograms per g leaf mass and 24 h) are cheaper to produce than EFN (usually produced in milligrams of sugars per g and 24 h). These latter considerations would favour hypothesis two: aspen plants that are infested by autumn moth caterpillars lose too much of their photosynthetic tissue and are therefore limited in their capacity for EFN secretion. Have Li and colleagues found an adaptive strategy of a generalist herbivore to suppress a common resistance trait that it is likely to face on multiple hosts? Or do we see here the first (albeit indirect) evidence for substantial metabolic costs of EFN secretion? The available data do not allow for a final decision on this question. However, the observations made by Li *et al.* (2012) certainly open future research avenues. For example, future studies could measure EFN secretion by other plants in response to *E. autumnata* feeding and EFN secretion by aspen after feeding by different herbivores. Similarly, indirect defences could be quantified under conditions that do, or do not, limit photosynthesis. More biodiversity in our experimental study systems and following Li *et al.* (2012) in the willingness to publish unexpected (or 'negative') results will increase our understanding of the circumstances under which a certain plant–

herbivore interaction elicits specific plant responses, and to identify the species that manipulate such interactions at their own benefits.

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