



How herbivores coopt plant defenses: natural selection, specialization, and sequestration

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We review progress in understanding sequestration by herbivorous insects, the use of plant chemical defenses for their own defense. We incorporate sequestration into the framework of plant–insect coevolution by integrating three hierarchical issues: (1) the relationship between dietary specialization and sequestration of plant defenses, (2) the physiological mechanisms involved in sequestration, and (3) how sequestration evolves via interactions between trophic levels. Sequestration is often associated with specialization, but even specialized sequestration is not an evolutionary dead-end. Despite considerable progress in understanding physiological mechanisms, detailed knowledge of how plant toxins cross the insect gut epithelium is still largely lacking. Sequestration is likely a major vehicle for coevolutionary escalation in speciose plant–insect–predator interactions, suggesting that a strictly bitrophic view is untenable.

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Introduction

Sequestration is a common phenomenon among herbivorous insects [1] and is defined as ‘the selective uptake, transport, modification, storage and deployment of plant secondary chemicals for the insect’s own defence’ [2]. While not all of these criteria are necessary for sequestration, the uptake of toxins typically connects the first trophic level (plants) via the second trophic level (insect herbivores) to the third trophic level (predators and parasitoids) and as such is an important force shaping ecological networks and evolutionary trajectories. From the perspective of such food chain interactions, the processes by which any

chemical compound is acquired and used by an organism are essential to understand.

All heterotrophic organisms are exposed to a wealth of chemical compounds in their diet and selective uptake and incorporation of these compounds is vital. For example, nutrients are critically needed, while uptake of detrimental compounds like toxins should be avoided. This selectivity has natural limitations, as uptake of nutrients involves physical and biological mechanisms which are not absolute in their specificity [3]. Amino acid transporters, for instance, may also transport toxic non-protein amino acids [4,5] and the permeability of the gut epithelium for essential lipophilic compounds will also allow for diffusion of toxic organic molecules (Figure 1). In the context of antagonistic insect–plant coevolution, limits on the specificity of uptake have likely been the target of natural selection, both from the plants’ and insects’ perspective.

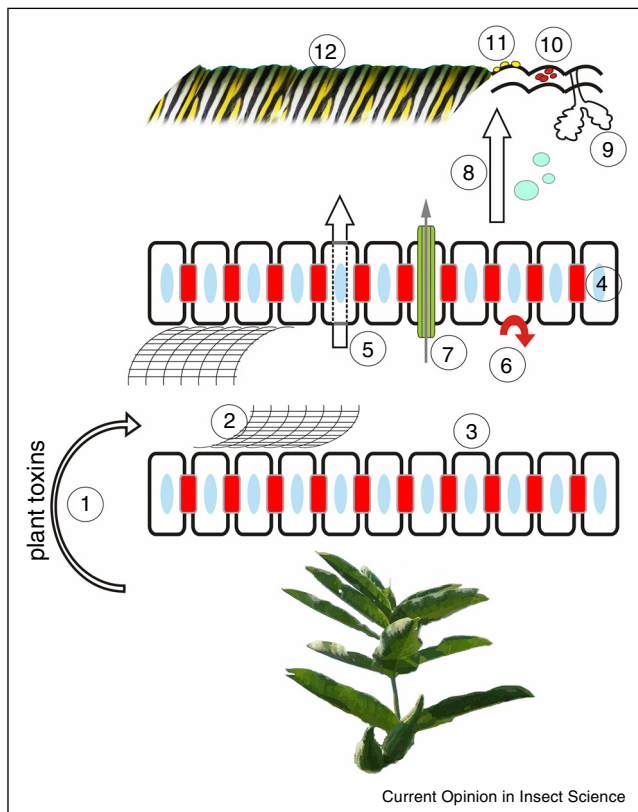
Selectivity of uptake can be realized by one or by a combination of many mechanisms. After ingestion, which itself can be selective based on gustatory discrimination, uptake of a compound across the gut epithelium can be prevented by either passive or active barrier mechanisms (e.g. diffusion barriers mediated by septate junctions or ATP-consuming efflux carriers like p-glycoproteins, see Figure 1) [6,7]. Moreover, a compound can be degraded in the midgut or in the body cavity and subsequently excreted via Malpighian tubules and defecation [2]. Absorption of a compound into the haemocoel can be passive (e.g. by diffusion of lipophilic compounds) or could be mediated by active carriers. The interplay of these physical and biological parameters will determine how much of a compound will enter the body cavity and how much of it will be discarded. Accordingly, the extent of selectivity via various mechanisms provides the physiological template for sequestration.

Despite its base at the plant–herbivore interface, at its heart sequestration must be considered in a tri-trophic context, both in terms of ecological outcomes as well as evolutionary drivers of species interactions. Thus, in this paper we integrate a trophic perspective in the framework of sequestration and review recent progress in understanding (a) how sequestration relates to dietary specialization, (b) the physiological mechanisms of uptake and storage of plant toxins, and (c) how sequestration evolves in a tri-trophic context.

Sequestration and dietary specialization

Just like dietary specialization, sequestration also requires resistance traits specific to sequestered plant toxins, and

Figure 1



Physiological mechanisms involved in sequestration. Upon feeding plant toxins are ingested (1) and contact the peritrophic envelope (2). The peritrophic envelope may be involved in the process of sequestration as plant toxins could bind to the envelope and toxins could be retained in the gut. It thus will prevent some toxins from reaching the gut epithelium and prohibit sequestration. The gut epithelium (3) represents the next layer of selectivity and sequestration may be modulated by active and passive barrier functions as well as metabolism by degrading enzymes and selective uptake. Polar toxins cannot be sequestered passively as paracellular diffusion across the midgut epithelium is restricted by septate junctions (4). Non-polar (lipophilic) compounds can be sequestered passively as they can cross cell membranes (5). Proteins like efflux carriers (6) mediate an active barrier to prevent toxins from reaching the body cavity [6]. One possibility for how polar toxins can be sequestered is via specific carrier proteins (7) [16,21]. The involvement of carriers in sequestration of plant compounds from the gut lumen into the haemocoel has been suggested but has not been functionally demonstrated at the level of individual carriers. Within the haemolymph, sequestered plant metabolites can be metabolized [2]; potential binding to haemolymph proteins or sequestration into haemocytes has not been investigated to date. Some toxins are transported across the haemolymph (8) into glands (9) [20*], reservoirs [25] or into the integument [8*] where they are stored (10) or exposed to predators (e.g. in the form of droplets, (11) [26]). Protection mediated by sequestered plant toxins is often displayed by aposematic coloration (12). Although advertisement of protection/unpalatability can be signaled via other modalities, aposematic coloration points to the importance of visually oriented predators (e.g. vertebrates) as evolutionary drivers for sequestration.

recent work has shown that these traits can differ from those primarily involved in eating toxic plants [8*]. Beyond simple consumption, sequestration requires adaptations

for the transport, metabolism, and storage of the toxins, and often to advertise and deliver the same compounds (Figure 1). In contrast to overcoming a plant toxin simply to use a dietary resource, which could be driven by pairwise coevolution, sequestration is typically driven by predators and parasites (the third trophic level). Thus, sequestration provides a link for how higher trophic levels can engage in coevolutionary interactions (Figure 2, [8*,9]) and can influence host plant associations. As it is increasingly recognized that sequestration is a common phenomenon, it may well be a second vehicle of coevolutionary escalation between plants and insects causing resistance adaptations necessary to tolerate sequestered toxins.

A bitrophic coevolutionary view of species interactions suggests that specialization is a consequence of escalating evolutionary antagonism. Although it is unclear whether sequestration follows specialization or vice versa, the two traits are often coupled. In feeding trials involving a comparison of 70 tropical caterpillar species, Dyer [10] showed that specialist caterpillars are less palatable to ant predators compared to generalist caterpillars. On the basis of these results it was suggested that predation could be a substantial selective force for the evolution of specialized feeding behavior and sequestration. Indeed, ant choices were mediated by the chemical composition of caterpillars, which was clearly derived from host plant chemistry.

More focused experimental evidence on single classes of compounds also indicates a relationship between sequestration and the degree of dietary specialization. For example, Lampert and Bowers [11] and Lampert *et al.* [12] compared sequestration of iridoid glycosides between the specialist Buckeye caterpillar *Junonia coenia* and several more generalized feeders; the specialist sequestered dramatically more iridoid glycosides compared to the other species. The same pattern seems to hold for phloem sucking aphids. Züst and Agrawal [13*] recently demonstrated that among a gradient of dietary specialization four aphid species on the milkweed host *Asclepias syriaca*, sequestration of cardenolides increased from the generalist *Myzus persicae* to the more specialized *Aphis asclepiadis* and *A. nerii*, and was highest in the monophagous *Myzocallis asclepiadis*.

The hypothesis that specialists sequester more efficiently than generalists also holds true in phylogenetically controlled comparisons. Engler-Chaouat and Gilbert [14] showed that several specialized species of *Heliconius* butterflies in the same clade sequester higher concentrations of simple monoglycoside cyclopentenyl cyanogens from their host plants (*Passiflora* spp.) as compared to *Passiflora* generalists fed the same plant species. These results suggest that herbivores with narrow diet spectra are more likely to sequester (or sequester more efficiently) as compared to those species which are less restricted in their host plant use.

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