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Sequestration of plant secondary metabolites by insect herbivores: molecular mechanisms and ecological consequences

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Numerous insect herbivores can take up and store plant toxins as self-defense against their own natural enemies. Plant toxin sequestration is tightly linked with tolerance strategies that keep the toxins functional. Specific transporters have been identified that likely allow the herbivore to control the spatiotemporal dynamics of toxin accumulation. Certain herbivores furthermore possess specific enzymes to boost the bioactivity of the sequestered toxins. Ecologists have studied plant toxin sequestration for decades. The recently uncovered molecular mechanisms in combination with transient, non-transgenic systems to manipulate insect gene expression will help to understand the importance of toxin sequestration for food-web dynamics in nature.

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Introduction

Herbivores face numerous constraints that limit their growth and reproduction. Plant defenses on one hand reduce food digestibility and attack essential physiological processes in the herbivores [1]. Natural enemies on the other hand directly threaten their survival [2]. A popular hypothesis among ecologists is that the combination of these two forces is responsible for the fact that plants rather than herbivorous insects dominate terrestrial ecosystems [3,4]. However, a closer look at more specialized insect herbivores reveals that they have found ways to neutralize both forces simultaneously by redirecting plant defenses to protect them against their own enemies [5,6]. Sequestration, defined as the specific and selective uptake and accumulation of plant toxins, is likely a key capacity that determines the success or failure of insect

herbivores on well-defended host plants in natural enemy-rich environments [7].

Plant toxin sequestration as a means of self-defense has been well described for numerous herbivores [5,6]. Recent molecular advances have revealed how herbivores tolerate, transport and activate plant toxins (see ‘Graphical abstract’) [8]. In this review, we discuss these novel findings and explore how they may translate into a better understanding of the role of sequestered plant toxins in terrestrial food-web dynamics.

Tight evolutionary and physiological links between tolerance and sequestration strategies

Contrary to common detoxification strategies that rely on degradation and excretion, sequestering herbivores need to keep plant toxins functional [9,10]. A number of molecular strategies have been described that allow herbivores to tolerate plant toxins [8]. The monarch butterfly (*Danaus plexippus*) for instance tolerates plant cardenolides through leucine (111) to valin and asparagine (122) to histidine substitutions in the α subunit of Na⁺/K⁺-ATPase that reduces the sensitivity of the enzyme to the plant toxin [11,12]. This insensitivity allows it to take up cardenolides and concentrate them in its body. Interestingly, this so-called target-site insensitivity was shown to be more strongly associated with cardenolide sequestration than overall tolerance across different species of milkweed butterflies (Danaini) [13[•]]. For instance, certain Danaini tolerate cardenolides despite having a sensitive Na⁺/K⁺-ATPase, possibly by avoiding their accumulation in the hemolymph [14]. It is therefore conceivable that the amino acid substitutions primarily helped insects to resist their natural enemies than to tolerate the toxins [13[•]]. A recent comparative study of different milkweed bugs (*Lygaeinae*) revealed a tight evolutionary link between cardenolide tolerance and sequestration, lending further support to this hypothesis [15].

Functional connections between specific tolerance mechanisms and sequestration have also been documented glucosinolates, a class of plant toxins produced by the Brassicales that require β -thio-glucosidase, that is myrosinase, action to produce toxic isothiocyanates [16]. Sulfatases and nitrile-specifier proteins (NSPs) for instance are employed by various herbivores to reduce the production of toxic isothiocyanates from glucosinolates

[17–19]. However, these strategies result in deactivated breakdown products that cannot be used for self-defense. By consequence, glucosinolate-sequestering insects have developed specific strategies to stabilize the toxins, including non-disruptive feeding and inhibition of hydrolysis [10,20].

A third example comes from plant cyanogenic glycosides that are hydrolyzed to toxic hydrogen cyanide (HCN) upon tissue disruption [21]. Many organisms can detoxify HCN, for instance through β -cyanoalanine synthase activity [22]. Sequestering insects on the other hand have evolved strategies to stabilize the glycosides and avoid uncontrolled HCN formation. Larvae of the burnet moth *Zygaena filipendulae* for instance combine leaf-snipping with a highly alkaline gut to suppress plant hydrolases [23].

Together, these recent studies show that secondary metabolite sequestration is associated with specific tolerance strategies that allow the herbivores to maintain the functionality of the toxins and tolerate their presence in the body. It should be noted however that not all tolerance strategies that are compatible with sequestration are necessarily associated with this trait. Benzoxazinoids for instance, which are activated by plant β -glucosidases upon tissue disruption, are stabilized through reglycosylation by non-sequestering *Spodoptera* species [24,25]. Also, a group of *Lygaeinae* seems to have lost the ability to sequester cardenolides, but has kept the associated Na⁺/K⁺-ATPase target site insensitivity [15]. Thus, sequestration needs specific tolerance strategies, but not *vice versa*.

Molecular insights into plant toxin transport

Plant toxins need to be moved out of the gut into the insect body to be sequestered effectively. A recent study on the poplar leaf beetle *Chrysomela populi* has identified an ATP-binding cassette (ABC) transporter (*CpMRP*) which is highly expressed in the defensive glands and transports the plant-derived phenolglucoside salicin *in vitro* [26**]. Knocking down *CpMRP* by RNA interference (RNAi) strongly reduced the defensive excretion of the beetles, suggesting an important role of this transporter in regulating the production of defensive liquid. On the basis of the literature, the authors proposed a model in which glucosylated plant secondary metabolites are transported across the gut membrane non-selectively followed by a highly selective transfer into the secretory cells and a controlled secretion into the defensive reservoir [26**,27]. Whether non-specific transport across the gut membranes is a general feature of sequestration systems remains to be determined. Other herbivores show highly specific secondary metabolite accumulation patterns in their hemolymph [28–30] suggesting specific transport. The identification of the molecular transport mechanisms in these herbivores would be necessary to confirm this hypothesis.

In *Manduca sexta*, a cytochrome P450 gene (CYP6B46) was recently identified to be required for plant-derived nicotine to pass from the midgut into the hemolymph [31*]. It remains unknown whether CYP6B46 is part of a multicomponent pump that converts nicotine into an intermediate transport-form that crosses the gut and is then converted back to nicotine or whether it influences nicotine transport *via* a different mechanism [31*,32]. Clearly, much is to be learned regarding the mechanisms of plant toxin transport in herbivorous insects. The identification of the first enzymes that are required for toxin transport may facilitate future efforts to identify and characterize transport systems [33].

Toxin activation by specialized enzymes

To function as effective anti-predator defenses, certain stabilized toxins need to be activated. The cabbage aphid *Brevicoryne brassicae* for instance produces a compartmentalized thio-glucosidase which can cleave the sequestered glucosinolates and release isothiocyanates upon tissue disruption [34]. Similarly, the leaf beetle *Phyllotreta striolata* produces a thio-glucosidase which can hydrolyze glucosinolates [35*]. In contrast to *B. brassicae*, *P. striolata* releases glucosinolate breakdown products also in the absence of cellular damage, possibly as a pheromone component [35*]. The two glucosinolate thio-glucosidases seem to be the product of convergent evolution [35*], suggesting that the capacity to activate plant toxins is an important component in sequestration systems.

Another example of toxin activation that is well understood on a molecular level is the conversion of salicin to salicylaldehyde by Chrysomelid beetles. A β -glucosidase and a salicyl alcohol oxidase (SAO) are responsible for this conversion in *Chrysomela lapponica* [36]. SAOs in the *Chrysomela* and *Phratora* are likely to have a common evolutionary origin and to have evolved through gene-duplication followed by neo-functionalization [37]. Strikingly, *C. lapponica* populations that feed on salicin free birch have strongly reduced SAO mRNA levels and express a non-functional SAO [36]. This suggests that the expression of the salicin activating enzyme is maintained through the presence of the compound and indirectly by the benefits that the enzyme product conveys. On the other hand, neither SAO nor salicin are strictly required for the survival of *C. lapponica* living on birch trees.

Translating molecular insights into ecological patterns

A major aim of herbivore ecology is to understand the spatial distribution and abundance of herbivores as a function of top-down and bottom-up processes. The sequestration of plant secondary metabolites by specialist herbivores is likely important for both [7], and we propose that understanding the molecular mechanisms of plant toxin sequestration will help to decipher food-web dynamics in terrestrial ecosystems. Although only a handful of studies

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