Does plant trait diversity reduce the ability of herbivores to defend against predators? The plant variability–gut acclimation hypothesis

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Variability in plant chemistry has long been believed to suppress populations of insect herbivores by constraining herbivore resource selection behavior in ways that make herbivores more vulnerable to predation. The focus on behavior, however, overlooks the pervasive physiological effects of plant variability on herbivores. Here we propose the plant variability–gut acclimation hypothesis, which posits that plant chemical variability constrains herbivore anti-predator defenses by frequently requiring herbivores to acclimate their guts to changing plant defenses and nutrients. Gut acclimation, including changes to morphology and detoxification enzymes, requires time and nutrients, and we argue these costs will constrain how and when herbivores can mount anti-predator defenses. A consequence of this hypothesis is stronger top-down control of herbivores in heterogeneous plant populations.

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Introduction

Insect herbivores face astounding variability in nutritional and defensive chemistry among potential host–plant species, among plants within host species, and even among tissues within single plants [1,2•,3]. Ecologists have long sought to understand the consequences of plant heterogeneity for interactions between herbivores and their predators [4]. Most work has focused on the indirect effects of diversity on herbivores that occur because plant diversity can directly benefit predators (Root's enemies hypothesis [5]). Only one hypothesis addresses the direct effects of plant variability on the responses of herbivores to their predators. The hypothesis, proposed by Schultz [6], posits that plant trait variability constrains herbivore movement behavior in ways that increase exposure to predators. Recent work, however, indicates that the relationship between plant diversity and herbivore movement is less clear-cut than originally thought [7••] (Box 1). More importantly, the focus on herbivore behavior overlooks the physiological effects of plant variability on herbivores, which we argue will scale up from the organismal level to influence herbivore–predator interactions at the community-level.

The plant variability–gut acclimation hypothesis

In this synthesis, we propose the plant variability–gut acclimation hypothesis, which posits that plant chemical variability constrains herbivore anti-predator defenses by requiring herbivores to undergo slow and costly acclimation to changing plant chemistry. Herbivores experience plant variability as they move among plants or organs within plants, or as the quality of a host–plant changes through time because of plant ontogeny or induced resistance [2•,8,9]. We bring together evidence from the literature on the physiological responses of the herbivore gut to plant variability and from the literature on the behavioral and physiological responses of prey to their predators. We argue the evidence indicates that (1) herbivores undergo gut acclimation in response to changing plant defenses and nutrition, (2) acclimation incurs time and nutrient costs, and (3) time and nutrient costs constrain how and when herbivores can mount anti-predator defenses (Figure 1). While we find solid evidence for each of these steps, data integrating all three are lacking. We walk through evidence for each step in turn and conclude by suggesting ways to study the full interaction pathway. Such research would elucidate a novel mechanism for how plant trait diversity influences interactions between herbivores and natural enemies and help explain why the strength of top-down control varies among ecosystems. We focus here on how herbivore gut acclimation may influence the responses of herbivores to predators; we leave for future work the important task of evaluating the relative importance of our hypothesis and the variety of other ways plant trait diversity has been proposed to affect herbivores and their enemies [4,10–12,13•].

Insect guts acclimate to plant conditions

Insects have an amazing capacity to reshape their digestive phenotype in response to the changes in nutritive and defensive chemistry they experience as they move among plants or among organs within single plants or as the

Box 1 The plant variability–herbivore movement hypothesis [6].

Schultz [6] proposed a hypothesis for how intraspecific plant variability influences interactions between herbivores and their predators due to herbivore movement behavior. This hypothesis, which we call the plant variability–herbivore movement hypothesis, posits that plant trait variability forces foraging herbivores to move more frequently and make longer movements between patches of high quality plant tissue. The hypothesized consequences are (1) increased encounter rates between herbivores and natural enemies and (2) aggregated distributions of herbivores that facilitate enemy foraging — both of which would increase top-down control on herbivores. This also means that plant variability prevents herbivores from using behavioral plasticity — reducing their movements and hiding — to reduce their predation risk. Schultz's [6] hypothesis can be viewed as extending Root's [5] resource concentration hypothesis to include the effects of natural enemies at fine scales. The resource concentration hypothesis [5] posits that increasing plant diversity decreases the mean size of suitable resource patches, and that smaller resource patches encourage herbivores to leave patches more frequently. Schultz [6] took this hypothesis one step further by applying it to intraspecific plant trait variability and pointing out that increased movement will alter interactions with natural enemies. There is abundant empirical evidence that movement makes prey susceptible to natural enemies [37–39], but the evidence for consistently positive relationships between plant diversity or variability and herbivore movement is equivocal [4,53]. Indeed, recent theoretical modeling indicates that a surprising variety of diversity–movement relationships are possible, including nonlinear relationships, depending on how plant cues at multiple scales influence herbivore colonization, within-patch movement, and emigration [7••]. To the best of our knowledge it remains unresolved whether or not herbivore spatial aggregation generally increases with plant trait variability, although theory suggests that plant variability due to induced resistance could lead to either even or aggregated herbivore distributions, depending on, among other traits, the lag time between feeding and induction [54].

quality of a host plant changes through time due to ontogeny or induced resistance. This includes plasticity in gut passage rate, gut length and mass [14,15], and types and concentrations of gut digestive and detoxification enzymes [16,17]. For example, grasshoppers (*Melanoplus differentialis*) feeding on low nitrogen diets for as little as three days will increase the relative size of their guts by almost 50%, which increases their digestive efficiency and allows them to maintain survival and growth despite the low quality of their diet [14]. When locusts (*Locusta migratoria*) were switched from a diet with a balanced protein:carbohydrate ratio to an imbalanced diet, they changed the concentrations of proteases and carbohydrases in their guts so that they continued to extract the optimum balance of nutrients despite the imbalance present in the diet [18]. Both beetles (*Leptinotarsa decemlineata*) and Lepidoptera (*Spodoptera exigua*) have been shown to respond to plant protease inhibitors, compounds that prevent the operation of specific protein digestion enzymes, by changing the identity of protease enzymes in their guts from proteases sensitive to the inhibitor present in the plant to proteases insensitive to the specific inhibitor [19,20]. Many species, including southern armyworms (*Spodoptera eridania*), have been shown to respond to

potentially toxic plant secondary chemicals by inducing the activity of mixed-function oxidases including cytochrome P450 monooxygenases, a broad group of enzymes that detoxify via oxidization in the gut [21–24]. The responses of cabbage looper (*Trichoplusia ni*) to plant defenses are so specific that at least 1456 genes are differentially expressed in the presence and absence of tomato or *Arabidopsis* defenses, and less than 5% of these genes played a role in responses to defenses of both species [25•]. The lab studies mentioned above indicate that diverse species acclimate to changing diets. A vital remaining challenge is uncovering the spatial and temporal pattern of plant heterogeneity experienced by herbivores in field settings and showing how often this heterogeneity forces herbivores to undergo acclimation.
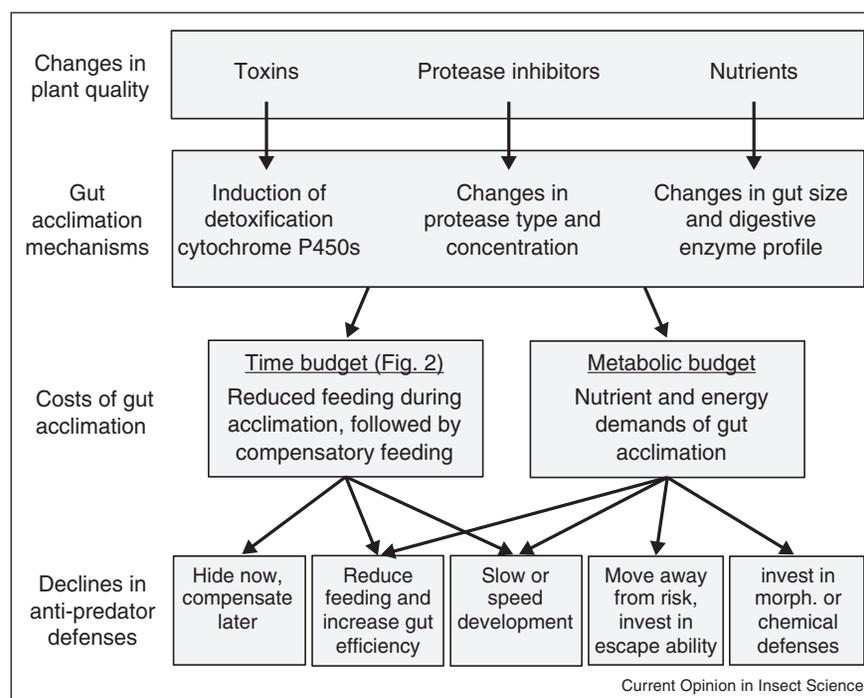
Gut acclimation has costs

There are two main costs of gut acclimation. First, gut acclimation takes time, and herbivores feed sparingly before acclimation is achieved. Second, it takes nutrients and energy to alter the size and quality of the gut. We review these costs by discussing examples from the literature on diet switching and induced host preferences.

Experiments on host-switching indicate that it takes herbivores many hours to several days to acclimate to new food plant nutritional and defensive chemistry, and a common observation is reduced rates of feeding before full induction is achieved [21,26–29]. For *Spodoptera eridania* introduced to a 0.1% sinigrin diet, it took 30 min to detect a significant increase in gut oxidase activity and 12–24 hours for the full induction response [21]. For *Manduca sexta* exposed to nicotine, full detoxification activity did not occur until 32 hours [28]. *Spodoptera frugiperda* reduced feeding time and number of feeding bouts by about 50% for a full two days while acclimating to a toxic but nondeterrent concentration of an allelochemical, but then resumed feeding at a normal rate after acclimation [29]. Spider mites (*Tetranychus urticae*), after two days of acclimation to a novel host, will have higher preference for and performance on that host [26]. Inhibitors of cytochrome P450 detoxification enzymes will prevent mite acclimation, indicating that P450 detoxification in the gut is integral to spider mite acclimation [26]. These results suggest that one challenge that herbivores face on novel hosts is a different profile of toxic secondary metabolites, and that herbivores respond to this challenge by reshaping the profile of P450 enzymes in their guts. The consumption lost while herbivores wait for full induction could become a significant cost for herbivores in variable populations of plants that require frequent changes to detoxification and digestive machinery.

The metabolic (nutrient and energy) costs of the phenotypic changes that take place in the gut during acclimation have rarely been quantified. In one of the best examples, Cresswell *et al.* [30] showed that detoxification

Figure 1

When herbivores experience a change in food plant defenses or nutrients (top row), they acclimate to the new conditions by reshaping their gut phenotype. Gut acclimation has time and metabolic costs, which may be minor in the absence of predators. In the presence of predators, we hypothesize these costs will reduce the ability of herbivores to mount common anti-predator defenses (bottom row) that rely on time, metabolism, or both.

of nicotine by *Spodoptera eridania* required assimilated food to be allocated from growth to energy metabolism, whereas previous studies had been unable to disentangle the negative effects of toxins on consumption and metabolism. Similarly, the parsnip webworm (*Depressaria pastinacella*), pays high metabolic costs to maintain P450 machinery even in the face of moderate starvation [31]. Indirect evidence for energetic costs of acclimation comes from studies showing reductions in feeding and mass gain when individuals are transferred to a new host plant [32,33]. For example, the clouded sulphur (*Colius philodice*) experiences increased conversion efficiencies after acclimating to a host plant, but individuals forced to switch hosts after acclimation have lower growth rates and pupal weights, and longer development times [34]. Japanese beetles (*Popillia japonica*) have lower rates of consumption when they feed among a diversity of host genotypes compared to when they feed in monotypic patches [35•]. Larvae of the salvinia moth (*Samea multiplicalis*) alter assimilation efficiency in response to changes in dietary nitrogen content, presumably to maintain growth on low quality diets [36]. However, individuals that experience variability in dietary nitrogen content are less able to take advantage of high quality, high nitrogen diets when they are available. This suggests that changes to the gut may be costly, or that these

herbivores are unable to change gut phenotype quickly enough to keep up with plant variability.

The examples in this section indicate that herbivore acclimation is common and costly in lab, greenhouse, and common garden settings. Studies are sorely needed on the importance of host–plant acclimation in field settings, where herbivore movement and resource-selection behavior are likely to play a larger role than they do in the lab. Potential costs of acclimation may or may not translate into fitness loses in safe environments, but below we argue that the costs of acclimation are likely to interact with predation risk in important ways.

The costs of gut acclimation limit the ability of herbivores to mount anti-predator defenses

The last component of the plant variability–gut acclimation hypothesis posits that the costs of responding to plant variability, described above, will limit the degree to which herbivores can mount anti-predator defenses and consequently increase the lethal effects of predation. While there is very little work that directly measures the effects of plant variability on herbivore responses to predators (with the exception of recent work on self-medication [13•]), we propose that there is an abundance of indirect

evidence suggesting that these effects are ecologically important.

The time costs of acclimation and time-based anti-predator defenses. Many common anti-predator defenses rely on plasticity in prey time budgets. This makes sense because of the widespread finding that prey are more vulnerable to searching predators when active and feeding and less vulnerable when inactive and vigilant [37–40]. For example, many species are inactive when they detect predators, and then compensate by feeding more after predators have left the vicinity [41,42]. When other species, such as *Manduca sexta*, face predation risk, they reduce consumption, spend more time hiding, and use physiological plasticity to increase gut efficiency, which allows them to maintain growth despite the reduced consumption [43••]. Another strategy for achieving normal body size at maturity despite risk-induced reductions in consumption is slowing development and extending the duration of the larval stage, whereas other species reduce the time they are exposed to predators by increasing consumption, speeding development, and shortening the duration of vulnerable life stages [44].

We propose that the hours to days it takes for herbivores to acclimate to changing plant conditions limits the ability of herbivores to use plasticity in their time budgets to exhibit the anti-predator defenses listed above (Figure 2). The result for the herbivore will likely depend on the relative timing of changes in plant quality and periods of relative safety and risk. If an herbivore were exposed to predation risk when it had already reduced feeding to acclimate to a new food plant, then it may not need to make any behavioral changes to further reduce predation risk. If an herbivore were exposed to predation risk after a period of acclimation-induced feeding reduction, then it may need to feed in spite of the risk of predation to compensate for the consumption missed during acclimation. In the former case, the costs of predation would be minimal because they would be redundant with effects due to plant variability, whereas in the latter case the herbivore would be unable to reduce its risk of predation, thus potentially increasing mortality due to predation. Recent theory predicts that when herbivores will be forced to resume feeding despite predation risk versus when they will be able to continue hiding will depend on the length of time an herbivore can survive on its energy reserves alone relative to the frequency with which resource quality and predation risk change [45••]. Clearly, future work in this area should measure the natural time scales of changing plant conditions and changing predation risk in relation to the rate of herbivore acclimation.

The threat of predation may also feed back to shape the amount and type of plant variability that herbivores encounter. Herbivores that move to avoid predators may experience relatively more spatial variability

Figure 2
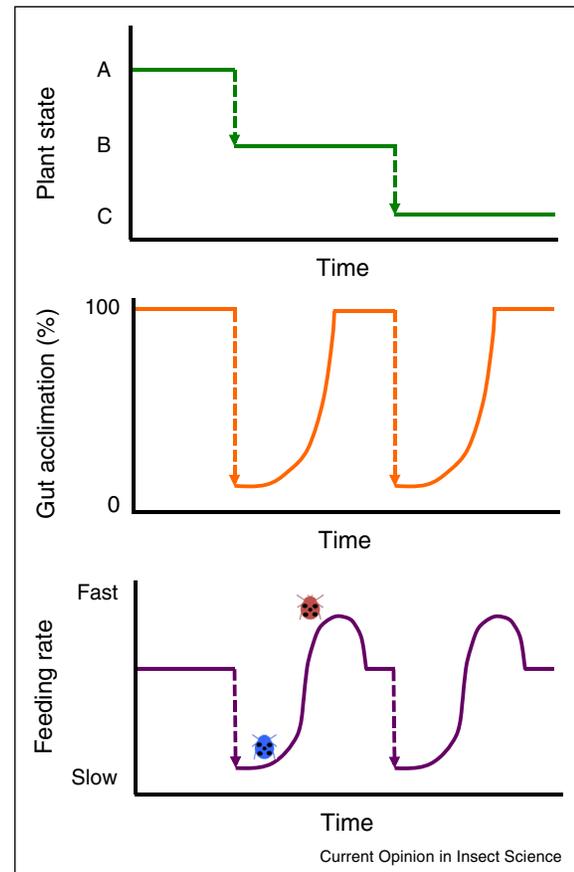
The timing of herbivore gut acclimation places a constraint on the timing of herbivore feeding. (Top panel) An herbivore experiences two changes in food plant conditions through time, from A to B and then from B to C. The plant states have different nutritional and/or defensive traits but are not necessarily better or worse quality. The changes could be due to herbivore movement among plants or tissues, or temporal changes like plant ontogeny. (Middle panel) The herbivore is initially acclimated to A. Acclimation drops when the herbivore switches from A to B. The herbivore then acclimates to B. This repeats for C. (Bottom panel) The herbivore reduces feeding while acclimation is low to avoid toxicity. It increases feeding with increasing acclimation until it feeds at a greater than normal rate to compensate for the loss of feeding during acclimation. The effects of the temporal constraints of gut acclimation on exposure to predators will depend on the timing of predation risk. If a predator arrives while the herbivore is acclimating (blue beetle), then it may cost the herbivore nothing to hide from the predator because it has already reduced its feeding. If a predator arrives after the herbivore has acclimated (red beetle), then the herbivore has to decide between the lesser of two evils: forgoing compensatory feeding to hide from the predator, or ignoring the threat of predation and continuing to compensate for the feeding deficit incurred during acclimation.

(e.g., due to plant genotypic diversity). Herbivores that reduce movement in the face of predation risk likely experience relatively less spatial variability and more temporal variability (e.g., due to induced resistance or plant ontogenetic changes).

The metabolic costs of acclimation and metabolic anti-predator defenses. Anti-predator defenses also make metabolic demands on the energy and nutrients available to organisms. Predator-induced stress physiology is a ubiquitous component of defense [46] and often increases and alters metabolic needs [47]. It typically leads to increased investment in mechanisms that increase the chance of surviving predators at the expensive of investment in other fitness components, such as resource acquisition and reproduction [48]. For example, tadpoles facing predation risk increase investment in tail muscles that facilitate rapid escape from predators [49]. This comes at the expense of investment in guts, and tadpoles under predation risk have smaller guts and are less efficient at resource acquisition, which may mean that they need to spend more time feeding. This illustrates that time-based and metabolic-based defenses are often interrelated. For example, the increase in assimilation efficiency *Manduca sexta* undergoes is likely only possible when it has resources available to invest in its gut [43••]. Similarly, increases in developmental rates, discussed above, rely on diversion of nutrients from storage (e.g., for reproduction) to development.

We propose that the metabolic costs that herbivores pay when they experience plant variability will limit their ability to mount anti-predator defenses. It is well established that prey have weaker responses to their predators and proportionally larger declines in density when in environments with low resource availability [50]. We have a much poorer understanding, however, of the effects of resource quality, but the little evidence that has accumulated suggests resource quality may be influential [51]. For example, *Manduca sexta* reduces its rate of consumption in the presence of predators on low resistance, jasmonate-insensitive tomato and on wild-type tomato, but not on high resistance, jasmonate-overexpressing tomato [52]. Consumption was already low on the high resistance plants, and presumably the herbivore could not afford to lower it any further. These studies show that resource limitation due to competitive interactions or plant defenses reduces the ability of herbivores to mount defenses. We are in need of studies that link all steps in the plant variability–gut acclimation and show that resource limitation due to plant variability can also reduce the ability of herbivores to mount defenses.

Conclusion

We believe that testing our hypothesis — that plant variability requires costly gut acclimation and reduces the ability of insect herbivores to mount anti-predator defenses — will require investigators to marry the field-based approaches used to study the ecological consequences of biodiversity with the mechanistic chemical and physiological approaches used in the field of plant–herbivore interactions. A vital task will be quantifying the spatial and temporal patterns of both plant trait heterogeneity and predation risk that herbivores experience in natural and agricultural ecosystems. Following on that, studies should manipulate plant heterogeneity at ecologically relevant scales, track herbivore physiology and behavior in the presence and absence of predators, and estimate the influence of plant heterogeneity on the strength of top-down control. Research that follows this trajectory will be ground breaking, whether or not it ultimately supports the plant variability–gut acclimation hypothesis, because it will for the first time reveal physiological mechanisms that shape the influence of plant trait diversity on herbivores and their interactions with predators.

Acknowledgements

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