

# Induced plant responses and information content about risk of herbivory

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Plant phenotypes change in response to past and present environments. Perhaps because plants are sedentary for most of their lives and cannot move away from dangerous locations, they respond to the environment in which they are rooted in other ways. Recent theory posits that plasticity will be favored only if plants can use information about their environments to respond appropriately. Traits are termed 'plastic' when a particular genotype has the capacity to produce different phenotypes. Here, we use the term 'information' without assuming any necessary benefit to the organisms involved (contrary to the definition used by many animal behaviorists<sup>1</sup>). Models of plastic plant phenotypes suggest that the past or current environment must provide information about future environments; plasticity might be favored only when plants can use this information to make the correct choice of phenotype on more than 50% of occasions<sup>2-4</sup>. More-recent models suggest that this threshold must be modified to include some consid-

eration of the fitness consequences (payoffs) of making the correct or suboptimal choices<sup>5-8</sup>. In other words, plasticity will be favored only if information is reliable and beneficial.

Plasticity involving plant defensive phenotypes with respect to herbivores is called an induced response. Over 100 plant species have been found to respond to past or current herbivory by increasing their resistance to herbivores<sup>9</sup>. In these studies, an initial attack acts as a cue for the plant to change its defensive phenotype, presumably because of increased risk of future herbivory. Induced changes in resistance can be favored by selection only if past or current herbivory is a reliable predictor of future risk of herbivory, and herbivory reduces plant fitness<sup>4,10,11</sup>. If the likelihood of herbivory is constant, and therefore predictable, selection should fix the defensive phenotype that is best for that set of conditions (although a varying phenotype might be favored for other reasons<sup>12</sup>). If the environment is completely unpredictable, and past or current conditions give no information about future risk, selection should fix the defensive phenotype that is best, on average, for that set of unpredictable conditions. However, if past or current conditions provide cues about the likelihood of future herbivory, selection might favor plants that respond to those cues and alter their defensive phenotypes.

**Plant defenses are plastic when a single genotype can produce different phenotypes depending upon the environment. Plastic responses might be favored by selection only if plants can respond appropriately to reliable information in their environments. Recent findings indicate that when information is accurate, plants can benefit by changing their defenses appropriately but, when information is inaccurate they produce inappropriate defenses and have lower fitness. Plants can potentially use a variety of cues to adjust their defensive phenotypes appropriately. The relationship between the information about risk of herbivory and plant defense can be evaluated by determining if the information available to plants is reliable enough to support the evolution of plastic-induced defenses.**

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Plasticity can be beneficial to plants when information is accurate, and costly when information is inaccurate. By stimulating wild radish (*Raphanus sativus*) and wild tobacco (*Nicotiana attenuata*) to induce resistance, plant lifetime fitness was increased<sup>13,14</sup>. However, this occurred only in environments that contained herbivores; in other words, where the information was accurate. In environments that did not contain herbivores, the signal to induce was inappropriate and plants that induced resistance suffered reduced fitness – a cost of induction<sup>14,15</sup>. A cost-benefit model that depends on information content is summarized in Box 1. Here, we consider several different sources of environmental information (cues) and the evidence that plants respond to each of these cues in nature (Table 1).

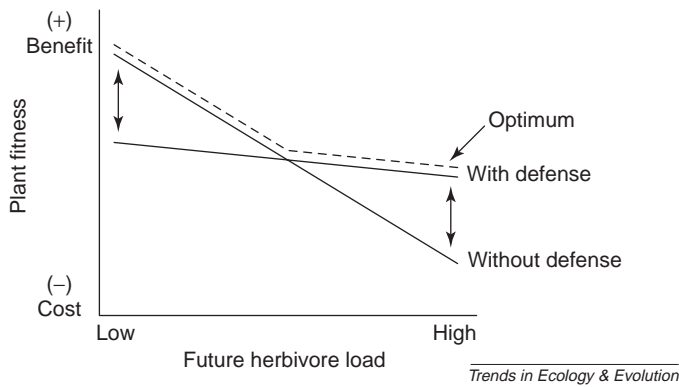
## Induced resistance when risk of herbivory is high

Past or current herbivory is the most direct cue about future herbivory. For this cue to provide reliable information, which plants

can use to respond appropriately, past herbivory must be a good predictor of future herbivory. This condition is fulfilled in several recent studies. Within a season, early damage to individuals of wild cotton, *Gossypium thurberi* by the primary folivore, a leaf miner, *Bucculatrix thurberiella*<sup>4</sup> is a reasonable predictor ( $R^2 = 0.30$ ) of the number of new mines that will be initiated during the rest of the season. Presumably, plants that are attractive and/or vulnerable to herbivores early in the season remain so throughout the season. There is no evidence in this wild cotton system that the reliability of information, based on early damage, decays as the season progresses. In other words, early damage provides information that is equally reliable about the risk that the plant would face several months later compared with several weeks later. Information about early season attacks, averaged from several shoots on a plant, provides a more reliable estimate of future risk to a single shoot than information from that shoot only. The number of mines produced by *B. thurberiella* provides the most reliable information about the likelihood of subsequent attacks, although chewing damage (caused by any of several herbivores) is a better inducer of resistance than specific damage by this herbivore. Nothing is known about correlations in risk of herbivory between seasons, although such data would be of great interest.

**Box 1. A conceptual framework relating the costs and benefits of plasticity to information content**

The hypothesis that the reliability of information about future herbivory affects plant fitness can be expressed as a simple model. We make three assumptions: (1) herbivores reduce plant fitness (i.e. the relationship between herbivory and fitness has a negative slope); (2) this slope (reduction in fitness) is less steep if the plant employs defenses; and (3) employing defenses is costly in terms of plant fitness (i.e. at the intercept, defended plants have lower fitness than undefended plants in the absence of herbivory). (Online: Fig. 1)



The predictions of the model are that correct information about future herbivore loads being low allows the plant to remain relatively undefended and thereby allows it to save the costs of unnecessary defense (double arrow on left); and that correct information about future herbivore loads being high allows the plant to reduce the costs of herbivory by increasing its defenses (double arrow on right). Many kinds of cues might provide the plant with reliable information about its future risk of herbivory (Table 1).

In this example, a plant can ‘assess’ whether it is in an environment where its risk of herbivory is great and then respond systemically to early season herbivory. Plants that are damaged early in the season become more resistant to caterpillars (reduced caterpillar performance) compared with plants that do not experience early season damage<sup>16</sup>. However, this does not affect the adult moth’s preference for these plants. This is important because a change in herbivore preference could confound the correlation between early and late damage. Sometimes, the risk of herbivory

varies greatly at a smaller spatial scale, for example, between branches of an individual plant. Branches can individually ‘assess’ whether they are likely to suffer herbivory and can respond locally to early herbivory. For example, in African *Acacias* browsed by mammalian herbivores<sup>17–19</sup>, spines are both inducible and effective at reducing this browsing. Spines are longer and denser on browsed branches; branches above the reach of herbivores are not browsed and produce much shorter thorns. Presumably, as shoots grow into branches they cannot ‘assess’, prior to damage, whether they are above the reach of their herbivores and, therefore, whether production of spines will be appropriate. Branches above the reach of herbivores are slow to relax their production of long spines, reflecting a ‘cautious’ strategy once they have experienced herbivory<sup>19</sup>. However, previous browsing is likely to be an information-rich cue and an excellent predictor of future browsing.

Induced resistance might be common in nature because early damage is often a good predictor of later risk. On a micro-scale, damage caused by first-instar caterpillars is likely to be a good predictor of herbivory by a later instar of that same caterpillar individual. Damage by herbivores that move little, and that have short generation times relative to those of their host plants [e.g. spider mites (*Tetranychus* spp.)], provides a reliable cue that the likelihood of later damage by subsequent generations of herbivores is great. To evaluate whether early damage is a reliable predictor of later damage, all that is required is a correlation between independent estimates of the levels of damage at these two time periods in the absence of an induced response. Surprisingly, very few studies have evaluated these correlations, in part, because induced resistance affects preference by herbivores in many systems, which complicates collection of independent estimates of damage.

**Reproduce rather than defend when risk is low**

In the previous examples, cotton plants and *Acacia* trees appear to abstain from employing defenses when they are not damaged. Presumably, lack of early damage provides information that risk of future damage is low. Under some circumstances, herbivory, rather than lack of herbivory, might also indicate that the risk of future herbivory is low. This could occur when herbivores are migratory: they will pass through an area only once during a season, although the precise timing of their migration might be unpredictable. Once they have passed, the probability of subsequent herbivory during that season might be greatly reduced. In this case, herbivory acts as a reliable cue that future herbivory is unlikely. We might, therefore, expect selection to favor plants that delay exposing vulnerable or preferred tissues until after the risk of herbivory has past. Such plants should use early season herbivory as a cue to reduce defenses and/or to produce vulnerable reproductive tissues.

Some populations of scarlet gilia (*Ipomopsis aggregata*) and footsteps of spring (*Sanicula arctopoides*) increase their production of flowers and fruits only after they have been grazed by elk or deer<sup>20,21</sup>. Similarly, some populations of field gentian (*Gentianella campestris*) produce more fruit and seeds after being grazed by horses<sup>22</sup>. In all three of these cases, the risk of herbivory is predictably high only once during the early season as a result of migratory herbivores. Populations of *I. aggregata* that experience herbivory later in the season, or experience more than a single bout of herbivory do not respond by reproducing after an initial bout of herbivory<sup>20,23</sup>. The plants might use early herbivory as a cue providing reliable information that migratory herbivores are gone and that subsequent risk of

**Table 1. Cues about risk that plants might use to adjust their phenotypes**

Cue <sup>a</sup>	Possible cue for:	Response	Refs
Past or current herbivory	High risk of future herbivory	Induce resistance	4, 17–19
Past or current herbivory	Low risk of future damage by migratory herbivores	Reproduce	20–22
Herbivores or cue of herbivores	High risk of future herbivory	Move to safer environment, change morphology	27–29
Predators of herbivores are present	Low risk of future herbivory	Reduce resistance	35,36
Hypersensitive response caused by pathogen propagule	High risk of future pathogens	Systemic Acquired Resistance	–
Abiotic environment	Risk of herbivory or pathogen attack is high or low	Induce resistance accordingly	42–47

<sup>a</sup>A cue provides information about the environment to the receiving organism<sup>1</sup>.

herbivory is diminished<sup>24,25</sup>. Plants might also delay producing vulnerable vegetative tissues (e.g. buds and new leaves) until after the risk of herbivory has passed, although this will be less readily observed than reproduction. To date, the number of examples in which plants appear to use lack of herbivory as a cue is limited.

### Herbivores as cues of a high risk of herbivory

In aquatic systems, water soluble chemical cues are used widely by predators and their prey to adjust behaviors and morphologies depending upon the likelihood of predation<sup>26</sup>. Although most of these examples involve animals, aquatic plants also respond to information about the presence of herbivores. For example, flagellated freshwater algae spend part of their life cycle as vegetative or resting forms at the sediment surface. They move into the water column where they reproduce and often come to predominate in the community. During periods of low herbivore abundance in the water, certain algal groups use cues released by herbivores to recruit from the substrate into the water column, effectively avoiding periods of high risk of herbivory<sup>27,28</sup>. In this system, waterborne cues associated with herbivores reliably predict the probability of future attack. Recently, several phytoplankton species have been found to change their colony size and to become more spined in response to cues released by their herbivores<sup>29</sup>.

### Predators of herbivores as cues of low herbivory

In the examples already mentioned, herbivores, or damage caused by herbivores, can provide information about the risk of herbivory. Where predators reduce herbivore numbers, predators might also provide cues that the risk of herbivory is low. Plants might use this information to relax their own defenses against herbivores. One example of this phenomenon involves ant-plant systems, in which ants provide an indirect defense for plants against herbivores and plants provide housing and/or food for ants. Most plants in ant-plant associations employ multiple defenses against their herbivores<sup>30</sup>. For example, *Cecropia* trees probably employ a combination of chemical (e.g. tannins and phenolics), physical (e.g. trichomes and leaf toughness) and biotic defenses (e.g. ants that feed on Mullerian and pearl bodies)<sup>31-33</sup>.

At least three environmental cues can provide plants with predictable information about the status of ants as potential defenders. These cues include the presence and/or absence of ants, abiotic (e.g. climatological) cues correlated with abundance of ants, and the current effectiveness of ants at providing defense. Ant-plants adjust their defensive phenotypes depending upon the strength of these cues. For example, *Cecropia* trees reduce their production of food bodies (a reward for ants), when ants are not present or are not harvesting the food bodies<sup>34</sup>. This change can be reversed by manually collecting the food bodies.

Abiotic conditions might also predict the presence or absence of ants and/or of particular herbivores. At high altitudes, where there are no ants, typically myrmecophytic plants enhance other defenses against herbivores. Individuals of *Bixa orellana* and *Inga* spp., growing above the altitudinal limit of ants, employ other physical and chemical defenses that are not found in plants growing at lower elevations where ants are present<sup>35,36</sup>. Predictably, other predators and parasites of herbivores do not exist at high elevation sites, and plants in these environments have foliage that is of lower quality to herbivores<sup>37</sup>. Cues associated with high elevation provide reliable information about

the risk of herbivory, although it is not known whether the different defensive phenotypes that were observed were caused by different genotypes or by phenotypic plasticity<sup>37</sup>.

If ants are present but ineffective, so that the plant is eaten despite its ant bodyguards, we expect plants to boost other defenses against its herbivores, by employing more conventional induced responses. Myrmecophytic *Endospermum labios* that has been colonized successfully by herbivores produces new leaves with more dense trichomes than plants lacking damage by herbivores<sup>38</sup>.

### Pathogens as cues about risk of future infection

Most of this review concerns plant responses to herbivores, but similar processes should apply to plant responses to pathogen attacks. Plants have multiple responses to attacks by pathogens and several of these are phenotypically correlated<sup>39</sup>. For example, when a plant recognizes a pathogen propagule, it initiates a localized hypersensitive response. In this response, the cells immediately surrounding the site of infection die, effectively trapping and cutting off the pathogen. These local responses also initiate systemic acquired resistance. Expression of these two processes are correlated so highly that, until recently, plant pathologists considered the hypersensitive response to be a necessary prerequisite for systemic acquired resistance, although they are now known to be regulated independently<sup>40,41</sup>. Because local hypersensitive responses are effective more often than not, it seems wasteful and redundant for the plant to use local cues to trigger systemic acquired resistance. However, encountering one pathogen propagule probably indicates that there is a high risk of encountering others. In other words, the plant might use information provided by its local response to one propagule to gear up its systemic resistance to other propagules. This is an effective strategy if, and only if, one encounter provides reliable information about the risk of future encounters. We are not aware of studies that have evaluated this hypothesis.

### Information about risk from abiotic factors

Plants in some environments are particularly prone to herbivory relative to individuals in other, safer environments. When the environment contains information about risk of herbivory, plants can use environmental cues to adjust their levels of defense. For example, plants in the sun might suffer a predictably higher risk of herbivory than those in the shade. This is the case for *Cardamine cordifolia*, because herbivores are consistently more abundant in sunny environments<sup>42</sup>. Experimental removal of shade causes plants to experience more herbivory and also to increase concentrations of glucosinolates (putative defensive chemicals)<sup>42,43</sup>. However, for plants that grow naturally in the shade, concentrations of glucosinolates remain low. Feeding by two species of adapted herbivores, chrysomelids and psyllids, is associated with lower concentrations of glucosinolates<sup>44</sup>. Thus, the sun predicts a high risk of herbivory to which plants might respond by producing glucosinolates, thereby increasing their resistance to herbivores.

Plant-water relations might also provide plants with information about their risk of attack by pathogens. It is well documented that the incidence of pathogen attack is higher under wet conditions than under dry conditions<sup>45</sup>. Many pathogens require high humidity to be infectious and are susceptible to desiccation. In addition, plants are often better able to respond to pathogen attack in moist environments than in dry environments. This is because abscisic acid, the plant hormone involved in plant responses

**Box 2. Testing the hypothesis that information is used to adjust phenotypes**

Plants growing in environments with a high risk of herbivory often have increased defenses compared with those growing in environments with lower risks (e.g. *Cardamine cordifolia* in sun and shade<sup>42–44</sup>). At least two hypotheses can account for the correlation between risk level and defense: (1) greater resistance in the sun results from selection imposed by herbivores; and (2) greater resistance in the sun results from other selection or physiological constraints (e.g. plants might have more resources to invest in defense when growing in the sun). These alternative hypotheses can be tested by finding systems in which there is the opposite correlation between the environment and risk of herbivory, predicted by the hypothesis that resources determine defense. For example, there are systems where risk of herbivory is higher in the shade than in the sun<sup>48</sup>. If environmental constraints shape the plant's phenotype in such a system then defensive traits should be observed in the sun (more resources) but not in the shade, even though herbivory is higher in the shade. If the risk of herbivory causes plants to modify their phenotypes then defensive traits should be observed in the shade but not in the sun, which is the case here<sup>48</sup>.

Another possible test of this hypothesis involves prickles in brambles. Deer feed preferentially in shaded environments and are presumably deterred by prickles<sup>49</sup>. Higher densities of prickles are found in shaded populations, counter to the expectation that plants in the sun will have more resources to make prickles. Plants might respond to herbivory by inducing greater prickle density, although the evidence for this induction is equivocal<sup>50</sup>. In this system, plants are responding to high risk of herbivory in the shade by producing more prickles, although the information cue (shade versus herbivory) and plasticity of the trait are uncertain.

These 'tests' apply specifically to the hypothesis that plants use information from the abiotic environment to adjust their phenotypes. This hypothesis is the least supported by biological evidence. The evidence is considerably better for plants that use information about the risk of herbivory, especially from previous herbivore loads, to alter their defensive phenotypes. Analogous 'tests' could be used to evaluate the hypothesis that this plasticity, triggered by cues of past herbivory, is adaptive. Comparisons involving single populations that show different phenotypes in different environments are always going to be subject to alternative explanations. Perhaps the best evidence will come from studies involving different populations of a single plant species that vary in their inducibility and also vary in the reliability of their cues. Because each population will represent a single data point, a large number of these populations will be required.

to drought, inhibits salicylic acid, the hormone involved in induced responses to pathogen attack<sup>46,47</sup>. Moisture level provides information about risk of pathogen attack and plants respond physiologically to match their defenses to this risk. In these examples, it is unclear if plants are responding to environmental cues or if the environment directly constrains the defensive phenotype. For example, plants growing in the shade might not be able to produce defensive phenotypes independently of cues or signals. A test of the 'adaptationist' hypothesis, which states that plants use information from their environments to adjust their defenses, is outlined in Box 2.

**Future directions**

All recent models argue that plastic or inducible defenses are favored where there is reliable information that plants can use to tailor their responses to match future risks. Information can come from a variety of different sources (Table 1). In the future, empiricists must answer the following questions. (1) How reliable is the information available to plants (e.g. is there a high correlation between the cues and future risk)? (2) Are induced responses beneficial when the information is accurate and costly when information is inaccurate? (3) Are plant responses to cues the result of selection by herbivores, adaptations to other selective forces, or shaped by physiological constraints?

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