

A comparison of plants and animals in their responses to risk of consumption

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Both plants and animals reduce their risk of being eaten by detecting and responding to herbivore and predator cues. Plants tend to be less mobile and rely on more local information perceived with widely dispersed and redundant tissues. As such, plants can more easily multi-task. Plants are more tolerant of damage and use damage to their own tissues as reliable cues of risk; plants have a higher threshold before responding to the threat of herbivory. Plants also use diverse cues that include fragments of plant tissue and molecular patterns from herbivores, herbivore feeding, or microbial associates of herbivores. Instead of fleeing from attackers, plants reallocate valuable resources to organs at less risk. They minimize unnecessary defenses against unrealized risks and costs of failing to defend against actual risk. Plants can remember and learn, although these abilities are poorly understood.

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Introduction

The essential challenges faced by plants and animals are quite similar — individuals must procure enough resources to grow, avoid becoming food for predators, parasites, and pathogens, and successfully transmit their genes to subsequent generations. They increase their chances of success by perceiving cues from their abiotic and biotic environments and altering their allocation to growth, defense, and reproduction. Behavior can be defined as this conditional, often reversible, cue-induced

change in phenotype [1^{••}]. Despite these fundamental similarities between plants and animals, many scientists have considered animals as uniquely capable of sensing and behaviorally responding to their environments.

Plants, as well as animals, perceive cues that are reliable predictors of current and future conditions [1^{••}]. Risk of attack by herbivores and predators is a particularly important environmental condition. Both plants and animals modify their allocation to defense when information can reliably predict risk of attack [2,3^{••}]. In this review, we identify the fundamental differences between animals and plants and argue that these differences causally shape how the two groups perceive, process, and respond to information regarding risk of attack (summarized in Figure 1). We compare plants to mobile animals with central nervous systems; sessile, clonal animals are more similar to plants in many regards.

Differences between plants and animals and how they shape behavior

Movement

Most plants require CO₂, water, and sunlight, rapidly renewable resources that can be obtained while sessile; most animals are forced to be much more mobile to obtain resources that renew slowly. As a result, many mobile animals move throughout relatively large areas (e.g., home ranges) and reduce risk by changing location. In addition, this difference in movement constrains the spatial extent of information that an individual can access. Plants are likely to receive most of their information from relatively nearby [4]. Movement differences between plants and animals also shape the mechanisms of perception. For example, plants benefit most from cues that operate over short spatial scales (e.g., volatile chemicals), whereas mobile animals also use cue modalities that provide information over greater distances (e.g., vision). Fundamental differences in movement also constrain the behavioral responses to risk for plants and animals (see below). A relatively small detection area means that plants have less time to respond before encountering an herbivore. Small detection area plus a slower response time make it harder for plants to mount effective induced defenses before being partially consumed.

Centralized versus decentralized perception and response

Plant bodies are not as specialized as animal bodies [5]. Animals are composed of specialized organs of which

Figure 1

Plants vs. Animals: Differences that shape responses to attack risk					
Trait → Consequences			Trait → Consequences		
	Perception	Response		Perception	Response
Highly mobile 	Collect information over larger area	Avoid risk; flee	Rooted in place 	Collect local information	Alter defenses and distribution of valuable resources
Single organs; non-redundant architecture 	Sense from single organ	Multitask less; pay opportunity costs	Modular organs; redundant architecture 	Sense from widespread, redundant organs	Multitask more
Little tolerance to attack or tissue loss 	Rely on pre-consumptive cues or long-range cues	Avoid attack; use caution; evolve cognitive abilities	Tolerance to attack and tissue loss 	Rely on damage to self and short-range cues	Induce defenses; reallocate resources

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Fundamental differences between plants and animals shape the ways they perceive their environments and respond (see also [75,76]). Plants, unlike animals, are less mobile (top), are constructed of repeated modular units (middle), and are more tolerant of attack and loss of some tissue (bottom). Low mobility leads plants to collect more local information and to respond by reallocating resources instead of moving. Modular architecture leads plants to have decentralized tissues that perceive cues and to be better able to multi-task. Tolerance to tissue loss allows plants to collect personal post-consumptive cues of risk and to rely on induced reallocation following attack.

there are one or relatively few copies (e.g., one brain, two eyes, one mouth). Plants are composed of multiple copies of redundant tissues and organs. Rather than two eyes located in the head, each leaf of a plant can be exquisitely sensitive to subtle variations in light quality and quantity. Plant meristems can give rise to almost any tissue at almost any time during development, providing plants with far greater morphological plasticity than most animals. This redundancy, decentralization, and plasticity allow plants to perceive risk and respond while carrying out other important tasks (e.g., foraging); animals, in contrast, often pay relatively large costs in terms of missed opportunities because time spent assessing and responding to risk cannot be spent on other activities.

Tolerance to attack

Plants are much more tolerant of herbivory than animals are of predation [3^{••},6]. Since plants are made up of repeated semi-autonomous units, they can afford to lose some of these tissues without suffering severe reductions in fitness. Undifferentiated plant meristems can replace damaged or missing tissue. In contrast, animals are much less tolerant of attack since removal of even small amounts of tissue is often irreplaceable and leads to loss of fitness or death [3^{••}]. These differences affect the mechanisms of perception because plants can use their own tissues to gain accurate information. Animals, in contrast, may make more sophisticated use of information obtained early in the attack

sequence and be under stronger selection for cognitive abilities allowing recognition and synthesis of information about risk before actual attack.

Cues about risk of attack

Both animals and plants perceive light, chemical, mechanical, sound, and electrical cues that provide information about attack risk [1^{••},7[•]]. These different sensory modalities provide information of varying quality that shapes the usefulness and reliability of cues for an individual animal or plant.

The modalities of sensing systems and cues are well-described for animals and we will build upon summary tables from this literature [7[•],8] to include plant sensing for comparison (Table 1). Several observations about these comparisons are worth noting. First, the relevant properties of cues (their range, how long they persist) are intrinsic to the cue and subject to environmental degradation; these properties are independent of the organisms that may perceive them. As a result, both plants and animals are sensitive to conditions that degrade cue reliability. For instance, plants in chronically windy environments may adjust their sensitivities and rely on constitutive defenses [9]. Second, plants have sensing systems that are functionally analogous to those of animals; these systems allow plants to perceive the same broad categories of cues [1^{••}]. Third, animal receptors are often

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