CONCEPTS & SYNTHESIS

EMPHASIZING NEW IDEAS TO STIMULATE RESEARCH IN ECOLOGY

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A judgment and decision-making model for plant behavior

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Abstract. Recently plant biologists have documented that plants, like animals, engage in many activities that can be considered as behaviors, although plant biologists currently lack a conceptual framework to understand these processes. Borrowing the well-established framework developed by psychologists, we propose that plant behaviors can be constructively modeled by identifying four distinct components: (1) a cue or stimulus that provides information, (2) a judgment whereby the plant perceives and processes this informative cue, (3) a decision whereby the plant chooses among several options based on their relative costs and benefits, and (4) action. Judgment for plants can be determined empirically by monitoring signaling associated with electrical, calcium, or hormonal fluxes. Decision-making can be evaluated empirically by monitoring gene expression or differential allocation of resources. We provide examples of the utility of this judgment and decision-making framework by considering cases in which plants either successfully or unsuccessfully induced resistance against attacking herbivores. Separating judgment from decision-making suggests new analytical paradigms (i.e., Bayesian methods for judgment and economic utility models for decision-making). Following this framework, we propose an experimental approach to plant behavior that explicitly manipulates the stimuli provided to plants, uses plants that vary in sensory abilities, and examines how environmental context affects plant responses. The concepts and approaches that follow from the judgment and decision-making framework can shape how we study and understand plant-herbivore interactions, biological invasions, plant responses to climate change, and the susceptibility of plants to evolutionary traps.

Key words: *cognition; defense; error; herbivory; information; psychology; signal.*

Introduction

Recently plant biologists have realized that plants, like animals, engage in a variety of plastic responses to environmental conditions that can be considered "behavior". These behaviors include foraging for light, water, and soil nutrients, and sensing and responding to potential competitors, herbivores, and mutualists (Silvertown and Gordon 1989, Trewavas 2014, Karban 2015, Mescher and De Moraes 2015). Plant behaviors are plastic responses to environmental conditions rather than fixed developmental programs or responses imposed by environmental or physiological constraints (Karban 2015, Mescher and Pearse 2016). Plant biologists since Darwin (1880) have recognized that many of these behaviors are analogous to those of animals. Since animal behavior as a discipline is older and better-developed, plant biologists may be able to make more rapid progress by borrowing perspectives, theory, and even methods from animal behaviorists. This reasoning has already been applied to plant foraging, communication, and defense against herbivores (e.g., Jensen et al. 2011, McNickle and Brown 2014, Orrock et al. 2015, Hilker et al. 2016). Psychology is an older and better-developed discipline than animal behavior and several scientists studying animal behavior have argued that psychology offers a conceptual framework and set of definitions that ethologists would do well to employ (Blumstein and Bouskila 1996, Mendelson et al. 2016). Here we propose that the framework used by psychologists can inform the nascent field of plant behavior.

Animal behaviorists who have looked to human psychology for transferrable insights have proposed splitting the processes that produce the emergent properties we think of as behavior into several identifiable (if not discrete) steps (Blumstein and Bouskila 1996, Mendelson et al. 2016). They have argued convincingly that treating the link between acquiring information and actions based on that information as a black box obscures the processes involved and leads to imprecise thinking (Fig. 1A). Only by understanding the components that make up the black box can greater clarity be achieved. We posit that decomposing these judgment and decision-making processes for plants will provide a similar benefit.

The judgment and decision-making (JDM) framework that has proven useful in psychology is likely to facilitate progress in plant behavior because plants, like animals, exhibit the key

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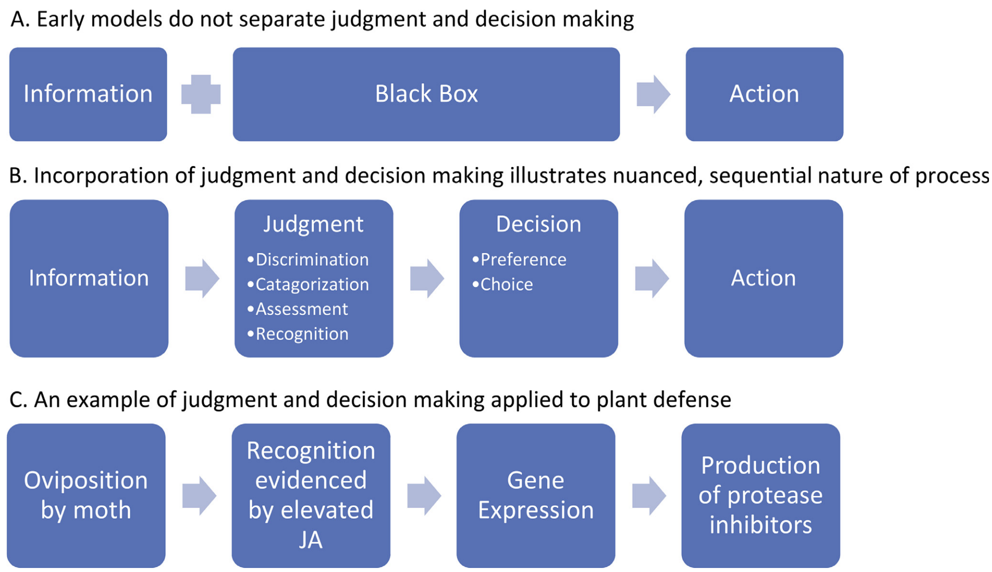

FIG. 1. Models of plant behavior. (A) An early model of behavior that treats cognition as a black box linking information with action. (B) The judgment and decision-making model developed by psychologists that has recently been applied to animal behavior (Blumstein and Bouskila 1996, Mendelson et al. 2016). This model breaks the cognitive process into two distinct steps: judgment that requires perception of information and decision that translates that judgment into action. Within the categories of judgment and decision making are additional distinctive terms used in animal behavior. Each of these terms represents unique phenotypic features that can be measured in terms of physiology of plant behavior. (C) An example of the judgment and decision-making model applied to induced responses of tomato plants to cues from eggs with oviduct secretions (from Kim et al. 2012). The plant perceives the eggs as evidenced by elevated levels of JA (judgment) and decides to act (gene expression), ultimately resulting in defense.

behaviors that constitute judgment and decision-making. Like animals, plants have receptors that detect information, plants process information (i.e., they make judgments regarding the state of the world around them), and plants respond to processed information by changing their phenotypes (i.e., they make decisions). For example, phytochrome and cryptochrome receptors sense the quality and quantity of light reaching a plant surface (Smith 2000, Casal 2013). These receptors trigger a cascade of different pathways that are mediated by phytohormones, primarily auxin, gibberellins, and ethylene. These hormones interact with each other and with other factors although auxin plays the main role activating and derepressing a suite of responsive genes that ultimately determine allocation to growth (Casal 2013, Weijers and Wagner 2016). Transcriptional, post transcriptional, and post translational controls allow feedback regulation and interactions with other hormones and environmental factors so that plants tailor their responses to the diverse cues that they receive. Decisions about resource allocation direct growth and reproduction in a manner that maximizes plant fitness (Dudley and Schmitt 1996). The decision making process is not as well understood yet for other plant functions, such as defense against herbivores (Karban 2015). In any case, the JDM framework is useful because it forces us to explicitly consider judgment and subsequent decision-making; this helps us understand how evolution has shaped the nature of perception and information processing and how organisms ultimately use information to make decisions related to fitness. In this regard, JDM helps us understand many phenomena: the evolution of sensory systems, the economics of individual choice, variation in decisions within and between species, and the response of species to novel stimuli and novel environments.

In this paper, we describe the JDM framework in the context of plants. We build on important earlier works (e.g., Silvertown and Gordon 1989, Gagliano 2015) to specifically integrate plants within a framework that includes human psychology (Goldstein and Hogarth 1997) and behavioral ecology (Mendelson et al. 2016). By doing so, we hope to facilitate a broader examination of the forces governing the evolution and ecology of information use among living organisms. In addition to this broad benefit, by helping us focus on the unique processes of judgment and decision making, this framework highlights areas where selection may (or may not) guide plant evolution, providing a clear focus for future studies (just as the framework does for animal studies; Mendelson et al. 2016). Finally, by helping us appreciate the similarities and differences in how plants and animals make judgments and decisions, the JDM framework facilitates additional novel study opportunities.

THE JUDGMENT AND DECISION-MAKING FRAMEWORK

Judgment describes how the organism processes information once it is detected (Fig. 1B, left side). Information can be acquired by sensing the current environment or by recalling past sensations (memory); discrimination, assessment, recognition, and categorization are all different components of judgment, and plants exhibit examples of all of them (Table 1). Judgment involves evaluating the stimuli that are perceived and inferring the state of the individual's current conditions. This process of judgment contrasts with decision making, which is using the information to determine a course of action (Fig. 1B, right side). Decision making involves evaluating the costs and benefits of alternative actions (or inaction). As such, decision making is often

TABLE 1. Components of the judgment and decision-making framework applied to plant behavior. Examples are provided corresponding to terms from behavioral ecology that were mapped onto the framework by Mendelson et al. (2016).

Component	Example
Judgment: Evaluating the stimuli that are perceived and inferring the state of the individual's current conditions	
Discrimination: a form of judgment in which plants distinguish between two (or more) alternatives	Root tips perceive concentrations of soil nitrate. The root then acts to continue to elongate if concentrations are low or stop and proliferate lateral rootlets if concentrations are high (Drew et al. 1973, Nibau et al. 2008)
Assessment: sensing information about the quantity and quality of a stimulus, rather than a comparison	A protein in the root tip of *Arabidopsis thaliana* can detect low levels of soil phosphorus (Svistoonoff et al. 2007)
Recognition: a form of discrimination that can be influenced by prior information or by past events	Venus flytraps must be stimulated by activation of two different hairs within 20 s of one another (Boehm et al. 2016)
Categorization: responding similarly to stimuli that share particular characteristics	Plants recognize the basic structural patterns of groups of microbes (Bent and Mackey 2007). When these patterns are encountered, the plant acts to mount a particular defense that corresponds to the specific pathogens (Zipfel and Felix 2005)
Decision: formulating a plan of action based on the costs and benefits of several options	
Choice: one option is selected from among multiple alternatives	Root tip of *Arabidopsis thaliana* senses an obstacle and causes a bend in the tissue above (proximal) to the tip so that the root grows laterally, thereby avoiding the obstacle (Massa and Gilroy 2003). The root chooses between two stimuli: gravity and touch. Tomato roots balance elongation vs. ability to penetrate (Santisree et al. 2011)
Preference: multiple options are presented and the plant ranks those options	Parasitic dodder seedlings preferentially grow towards tomato hosts (a good host) compared to controls with no host plant or wheat but will accept wheat over the control when no tomato is available (Runyon et al. 2006)

influenced by tradeoffs with different potential outcomes and comparisons of alternative actions (Orrock et al. 2015); decision making results in a plant exhibiting preference or making a choice (Table 1).

One important distinction between judgment and decision making clarifies the different evolutionary pressures that have likely shaped these two processes. Judgment should be shaped by accurate perception of the environment whereas decision making should be shaped by the relative costs and benefits of particular actions (given the accuracy of the judgment process) and the degree to which past and present cues predict future conditions. Distinguishing between these two drivers is useful because it can provide insight into the mechanisms that underlie a particular ecological or evolutionary observation. Plants that are incapable of making accurate judgments are unlikely to make optimal decisions without evolutionary intervention on perception and judgment; when judgment is accurate, plants may still vary in the decision-making process. For example, introduced plants may accurately judge the new environment, but may make choices based upon cost-benefit structures from their native range; selection operating on decision making could eventually lead to a highly successful invader.

Identifying judgment vs. decision making

The judgment and decision-making framework becomes more functionally useful in situations where it is possible to unambiguously identify when an individual has perceived a stimulus (e.g., made a judgment). Physiological measures such as eye tracking, heart rate, hormone levels, and neuronal spikes are accepted as accurate indicators that an animal has perceived a stimulus (Mendelson et al. 2016). Recent advances in plant physiology make it possible to determine if plants have perceived environmental information, with or without an active plant response. For example, plants sense many abiotic and biotic stresses and translate this information into electrical signals and fluxes of Ca^{2+} which move rapidly throughout the plant (Choi et al. 2016). The propagation of these wavelike signals indicates that the plant has perceived the stimulus, e.g., that the judgment part of the process has occurred. Just as animal biologists can use hormones to assess judgment (Nelson 1995), plant biologists can also evaluate judgment by measuring the dynamics of plant hormones. For example, defenses against herbivores often involve the hormone jasmonic acid (JA) and defenses against pathogens often involve the hormone salicylic acid (SA) (Felton et al. 1999, Thaler et al. 2012). Plants that exhibit increases in the appropriate hormone have perceived the potential threat (Fig. 1C). Their decision-making process can be understood by measuring their patterns of gene expression and defensive reactions that follow recognition of their environment (Figs. 1C and 2).

Using this framework: induced resistance to herbivory as an example

One of the main goals of plant defense theory is to understand why plants are highly defended in some situations and poorly defended in others (Feeny 1976, Rhoades and Cates 1976, Coley et al. 1985, Stamp 2003). The JDM framework helps to explain this variation, which involves perception, judgment, decision-making and action (Fig. 2). Plants respond to many informative cues that indicate the risk of herbivory including actual tissue damage, chemicals released by insects walking over plant surfaces, secretions associated with oviposition, and actual feeding (Karban 2015). The judgment phase involves plant signaling that includes membrane depolarization, Ca^{2+} fluxes, elevated MAP kinase activity, and reactive oxygen signaling. These early events

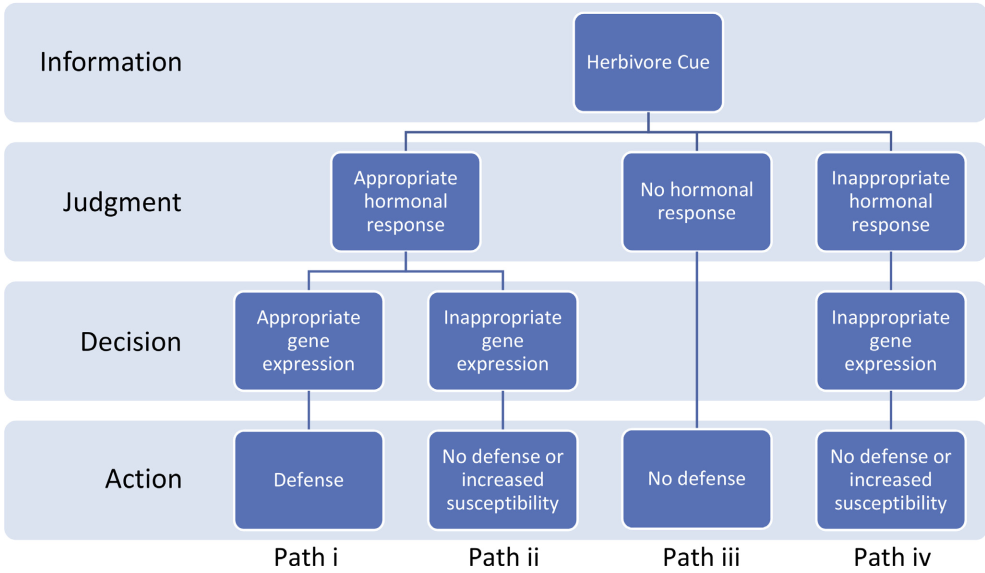

FIG. 2. A path diagram showing 4 possible plant responses to the same stimulus, a cue from an herbivore. Path i. – the plant recognizes the cue, and makes the decision to express genes that ultimately provide defense. Path ii. – the plant recognizes the cues but makes the decision to express genes that provide no defense or that leave the plant more susceptible to herbivory. Path iii. – the plant fails to recognize the herbivore and therefore fails to mount a defense. Path iv. – the hormonal response is inappropriate so that genes are expressed that fail to defend the plant or make it more susceptible to herbivory.

activate plant hormones (jasmonic acid, salicylic acid, ethylene, green leaf volatiles) and transcription factors. Many plant responses to herbivory are orchestrated by jasmonic acid which interacts with the other hormones. The decision-making process is less well understood although it results in changes in plant metabolism and allocation of those metabolites. The JDM framework leads to explicit, testable predictions regarding each of these components. These predictions can then be used to design field and lab experiments to evaluate whether these processes underlie the currently unexplained patterns in plant defense.

Incorrect judgment generates inappropriate action.—Application of the JDM framework clarifies how herbivores suppress plant defenses and helps inform future experiments. When cabbage butterflies, *Pieris brassicae*, oviposited onto the leaves of *Arabidopsis thaliana*, SA accumulated and levels of JA were depressed (Bruessow et al. 2010; Fig. 3A). This response indicated that the plants miscategorized the eggs as pathogens and this judgment led them to depress expression of genes that respond to the JA pathway. If insects suppressed plant defenses via changing the nature of decision making in plants (e.g., by introducing pathogens that might make a defensive response to herbivores too costly), an entirely different suite of future experiments would be indicated.

In a related example, Colorado potato beetles were found to contain bacteria in their oral secretions that caused tomato plants to categorize them as pathogens rather than herbivores (Chung et al. 2013; Fig. 3B). The tomato plants greatly increased levels of SA and decreased levels of JA, a judgment that was consistent with attack by pathogens but not attack by herbivores. This caused an increase in expression of SA genes and a reduction in expression of JA genes, and left the plant vulnerable to herbivory. When beetles were treated with antibiotics that removed the bacteria in their oral secretions, tomato plants recognized them as herbivores as evidenced by a small increase in SA; this categorization ultimately led to increased defenses that were effective against the beetles. In this case, the beetles were able to feed successfully on tomato plants by introducing bacteria that prevented the plants from accurately categorizing them as herbivores.

Appropriate judgments but herbivore-modified plant decisions.—When tomato plants were attacked by two-spotted spider mites, *Tetranychus urticae*, they increased levels of both JA and SA (Alba et al. 2015; Fig. 3C). These hormonal changes triggered expression of multiple gene families that led to effective induced resistance against these herbivores. However, when two mite species (*T. urticae* and *T. evansi*) attacked tomato simultaneously, the plants correctly recognized the attackers and increased both JA and SA levels but failed to express the appropriate genes needed to provide defense. JA-responsive genes such as proteinase inhibitors were not expressed and SA-responsive genes such as PR proteins were only slightly expressed. In this case *T. evansi* influenced the decision-making process and suppressed expression of defensive genes. The ability of *T. evansi* to influence the plant's decision clearly benefits this mite; this decision also allows tomato plants to prioritize faster reproduction which may mitigate some of the costs of herbivory under some circumstances (Liu et al. 2017). Pathogens also interfere with plants' decision-making process and the mechanisms of this interaction are better understood than those involving herbivores. For example, the bacteria *Pseudomonas syringe* injects a protein that degrades key regulatory proteins in the plant that are required for normal auxin responses (Cui et al. 2013).

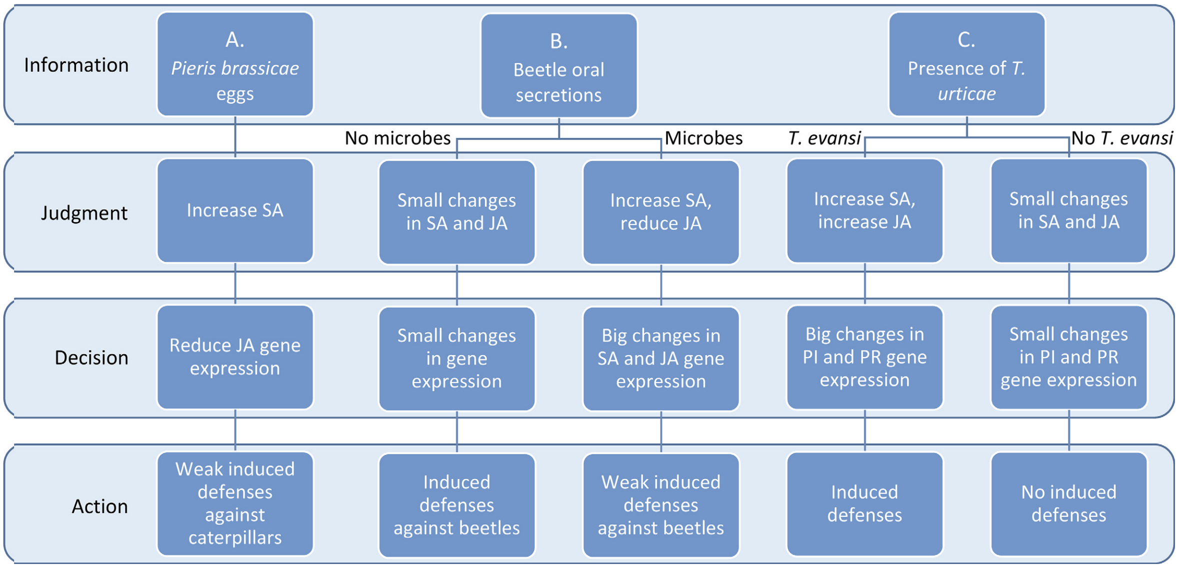

FIG. 3. Examples of the judgment and decision-making model applied to plants attacked by various arthropod herbivores. (A) When *Pieris brassicae* butterflies oviposit on *Arabidopsis thaliana* leaves, the plant misidentifies the butterflies as a pathogen and depresses expression of genes that provide defense against caterpillars (Bruessow et al. 2010). (B) Oral secretions from Colorado potato beetles (*Leptinotarsa decemlineata*) that contain bacteria cause tomato leaves to increase levels of SA and expression of SA genes (Chung et al. 2013). JA responses appropriate to herbivores are depressed, leading to weak defenses against the beetles. However, when antibiotics rid the oral secretions of bacteria, SA levels fail to increase and the tomato plants mount effective defenses against these herbivores. (C) Tomato plants that are attacked by *Tetranychus urticae* show elevated levels of both JA and SA that ultimately lead to induced resistance. However, when *T. urticae* and *T. evansi* both attack tomato plants the hormonal response is appropriate but the plant does not express genes that protect it (Alba et al. 2015).

Benefits of Incorporating Plants into the Judgment/Decision-Making Framework

A constructive analytical framework for plant biology

Psychologists and animal biologists who have attempted to model behavior have found that different research approaches are most useful for understanding judgment and decision-making. The measure of an individual's ability to judge the true state of its environment is accuracy; Bayesian approaches have been used successfully to model whether an individual is accurately updating its assessment of its surroundings (Hilborn and Mangel 1997). In contrast, the consequences of different decisions can be measured and compared using models of expected utility that were developed in economics (Edwards 1954). Plant biologists can only make use of these different approaches if they first recognize that behavior includes two different processes, judgment and decision making. Moreover, the explicit recognition of these two processes provides a useful perspective on existing questions in plant biology, and identifies interesting new areas for investigation.

Plants as tractable systems for understanding the ecology and evolution of information use

One benefit of incorporating plants within the judgment and decision-making framework which was developed for humans but recently applied to other animals (Mendelson et al. 2016) is that it highlights how plants might be used to test basic components of behavioral theory that are intractable or unethical to test in animals. For example, many of the chemical and physiological markers of plant pathways associated with the judgment phase are straight-forward to detect. As such, it should be possible to use genetic and comparative techniques to create plants with altered sensory abilities to evaluate the judgment process. Since decision making is context dependent it should also be possible to manipulate the plant's environment (e.g., fertilizers, competitors, herbivores) to alter the context. Combining these two approaches in factorial manipulations should allow controlled experiments to evaluate both judgment and decision making and to test behavioral theory more readily than with animal systems.

For example, risk sensitivity theory was developed by animal behaviorists to understand the conditions that favor risk-taking, that is, an organism's preference for a high- or low-variance outcome (Caraco et al. 1980, McNamara and Houston 1992). This theory predicts that individuals should be relatively risk-averse when resources are more abundant and risk-prone when resources are scarce. Experiments with animals have provided weak support for this paradigm (Kacelnik and El Mouden 2013) and human behavior is particularly difficult to reconcile with this theory (Schmid 2016). A significant constraint with testing theory using vertebrate or human subjects is linking decisions to fitness; this constraint does not apply to plants, particularly short-lived plants. Indeed, pea seedlings that were offered a choice between soil patches with constant and variable levels of nutrients provided strong support for risk-sensitive theory (Dener et al. 2016).

Judgment and decision making for animals vs. plants

The processes of judgment and decision making occur in the central nervous systems of animals, employing organs that plants completely lack. In plants, analogous processes occur in widely dispersed, redundant cells (Schmid 1990, Karban 2015), and decision making may be accomplished by democratic processes based upon competing inputs and needs of individual cells and tissues. For example, light triggers the synthesis of auxin, which accumulates in rapidly dividing and growing tissues (Ljung et al. 2001, Halliday et al. 2009). The relative levels of auxin export from various organs and tissues (shoots, roots, and so on) set priorities for resource allocation and growth. Positive feedbacks between auxin production and resource allocation allow for the most productive tissues to gain the most resources and grow the most rapidly (Sachs 1981, Domagalska and Leyser 2011). For example, because the cambium mediates the interests of various branches (Sachs 2006), it likely serves as the location where judgments regarding the needs of different shoots are formed and used as a basis for decisions regarding resource allocation to individual shoots. Those branches that are most productive and supply the cambium with the highest concentrations of auxin produce the most vascular tissue, which selectively provides them with resources while less productive branches are provided with fewer resources. In weighing inputs and needs in this way, the process of decision making in plants may be similar to collective decision making in social animals, (e.g., house-hunting by hives of bees [Seeley 2010], or ants [Franks et al. 2003]) and quorum sensing in bacteria (Miller and Bassler 2001). In these examples, and in plants, decision making arises by using a collective of widely distributed redundant sources which provides several benefits (Couzin 2009). By pooling judgments from multiple distributed sources plants may make more accurate decisions. Widely distributed sources of information and decision-making tissues may reduce the likelihood of catastrophic failure following perturbations since the success of decision making does not hinge on a few specialized and localized organs.

Although we know relatively less about the receptors that plants use to sense their environments (Karban 2015), it is clear that plant receptors are quite different from those used by animals. In general, responses of plants occur at a slower pace compared to animals (Silvertown and Gordon 1989), although it is unknown whether the temporal scale of these responses is analogous to the temporal scale of herbivore attack (which might also occur slowly; Karban et al. 2016). In addition, the types of actions that are available to animals and plants are rather different. For example, animals often respond to the risk of predation by fleeing (Orrock et al. 2015, Karban et al. 2016). Plants are rooted in place, making flight impossible so they respond to risk by reallocating resources, developing tolerance to partial tissue loss, and inducing defenses.

Differences between plants and animals in their means of acquiring and processing information result in differences in the decisions that they reach and the actions that they take. For example, we have hypothesized that plants and animals tend to have different decision-making thresholds (Orrock et al. 2015, Karban et al. 2016). Plants are more tolerant of loss of some tissue than are most animals, in part because plants are composed of redundant and semi-autonomous tissues and receptors. Loss of a plant branch is less likely to depress fitness than loss of an animal limb. Loss of the light receptors of one leaf is less likely to depress fitness than loss of one eye. As a result, plants often require actual damage to their own tissues before acting. Animals tend to be more cautious, acting in response to earlier, though possibly less reliable, cues.

JDM and insights into plant interactions with herbivores, pathogens, and mutualists

The JDM should apply to any interaction where the plant must integrate information from the environment and decide how to proceed. As we highlighted in the earlier section, the JDM framework helps formulate hypotheses to understand variation in plant defense against herbivores, a fundamental goal of plant-herbivore research (Agrawal 2011). For example, plants that do not respond to herbivore attack may do so because they lack the ability to detect a particular cue (e.g., saliva of an introduced herbivore). In such a situation, substantial evolution is likely to be required before an accurate judgment can be made (although biotechnology may hasten this process for crops). In this case, a natural population may go extinct before these evolutionary changes occur. If the receptors are in place but the sensitivity to the cue is inappropriate, fine-tuning is required and this is likely to occur more readily. Plants are sometimes faced with conflicting cues. As noted above, plants often respond to pathogens when herbivores are present. Evidence from many systems suggests that tradeoffs in signaling systems are common and these contradictory cues may present decision tradeoffs that are inevitable (Felton et al. 1999, Thaler et al. 2012). The cues themselves may be inaccurate or unreliable. In this case, we predict that selection will favor reliance on more information-rich cues. In many instances, the cues are manipulated by other vested organisms. In these cases, we predict that selection should favor the evolution of plant receptors that allow the plant to circumvent the manipulation by other organisms. For example, saliva from *Helicoverpa zea* caterpillars suppresses the recognition systems of many plants, although tomato has apparently evolved to correctly perceive this herbivore and appears to have generally won this evolutionary arms race, at least for the time being (Tian et al. 2012).

A plant may make an accurate judgment but an inappropriate decision. For example, variation in response to herbivores may arise due to the context-specific nature of the decision-making process. In one study, sagebrush responded to cues of herbivore risk more effectively when it was well watered compared to drier conditions (Pezzola et al. 2017). Decisions in response to cues may have context-dependent consequences that result in weak or stabilizing selection. For example, responding to a generalist herbivore may make the plant more attractive and/or susceptible to specialists (Poelman et al. 2010, Ali and Agrawal 2012). These conflicting consequences will reduce the benefits of responding. There are also examples of situations where the herbivore or another antagonist suppresses or otherwise manipulates the plant's decision making. *T. evansi* is thought to do this in the tomato example discussed above (Fig. 3C; Alba et al. 2015). We predict that this will present strong selection pressure for the plant to overcome.

It is interesting to note that herbivores that are able to manipulate plants into making decisions that prioritize local organs rather than the entire plant can exploit those plant decisions. For example, insects manipulate plants into producing galls, which provide the gall makers with highly nutritious food; although the precise mechanisms are not known, high concentrations of auxin and plant resources are associated with galls (Tooker and Helms 2014, Giron et al. 2016). In these cases, it seems likely that the gall maker is able to take advantage of plant pathways (e.g., decisions) that are highly conserved and difficult for the plant to do without or to modify (Giron et al. 2016). Similarly, herbivores that disrupt apical dominance in their host plants are able to manipulate plants into repeatedly prioritizing local regrowth to produce highly nutritious and poorly defended tissue instead of decisions that would benefit the entire plant (e.g., Craig et al. 1986, Potter and Redmond 1989, Craig 2010). In other instances, herbivores are successful because they target the communication systems that enable plants to make decisions and mount a collective plant-wide defense. For example, some specialist leaf feeders first sever the connections between tissues they consume from the rest of the plant, preventing both localized and systemic plant defenses (Dussourd 2009). In these cases, both the judgement and decision-making systems are directly compromised by the herbivore behavior.

One of the predictions of error management theory (Orrock et al. 2015) is that selection will favor the evolution of individuals that have a systematic bias to make judgment errors in a particular direction if the costs associated with that error are relatively small compared to the alternative. In the examples of plants that make mistakes in judgment, including the two that we discussed above (Bruessow et al. 2010, Chung et al. 2013), the plant mistook its herbivores for pathogens. In these cases we speculate that the risk of failing to recognize a pathogen is far greater than the risk of incorrectly identifying an herbivore. For example, none of the bacterial isolates found in the oral secretions of the Colorado potato beetles were actually pathogenic to plants (K. Hoover, *personal communication*). However, one of the elicitors that the tomato plants responded to was flagellin, a highly conserved cue that correctly identifies most pathogenic bacteria (Zipfel and Felix 2005). This bias in judgment is predicted from application of error-management theory to plant defense (Orrock et al. 2015) and illustrates the usefulness of examining plant behavior using a judgment and decision-making framework.

JDM may also provide useful insight into mutualistic interactions between plants and other organisms. For example, evidence suggests that mycorrhizal networks can alter the response of plants to herbivores (e.g., Gehring and Whitham 1994, Kempel et al. 2010). If mycorrhizae provide a more accurate description of the state of the world, they are improving plant judgment. If mycorrhizae change the costs and benefits of responding to that information, they may alter the decision-making process. An interesting possibility is that mycorrhizae provide unique information inputs (i.e., they provide unique cues or information modalities) that modify plant judgment (Song et al. 2010). Such modified judgment could benefit the plant and mycorrhiza, but might also represent a means of exploiting the plant when the mycorrhiza and the plant have different interests, as mycorrhizae may sometimes be mutualists, but sometimes parasites (Hoeksema et al. 2010, Kiers et al. 2011).

Insights into novel species interactions

In the future, organisms are likely to be placed into new ecological situations interacting with organisms with which they have little or no historical experience (Williams and Jackson 2007, Gilman et al. 2010). Their success or failure is likely to be affected by whether they have an evolutionary history that is well matched to the judgments and decisions that will be appropriate in the novel situation (Sih et al. 2011). For example, plants that have experienced herbivores similar to the novel herbivores that they will face as the result of anthropogenic changes are predicted to be more likely to recognize those novel species in order to defend themselves. Characteristics of a plant's ability to judge its environment lead to testable hypotheses about how it will respond to novel situations. For example, plants that rely on general cues of herbivores or damage are predicted to be more likely to recognize novel herbivores than are plants that rely on highly specific cues of particular risks. In general, the breadth of cues used by a plant species may predict successful judgment when it is faced with novel challenges. In situations where strong mismatches are expected to greatly affect population persistence, strategies proposed for mitigating inappropriate choices (evolutionary traps) for animal populations may promote plant JDM evolution and persistence. Specifically, creating refuge populations that are shielded from the novel agent of selection or intentionally introducing individuals from plant populations where JDM has successfully evolved into a naive population may promote persistence (Schlaepfer et al. 2005).

Herbivores are but one of many factors that may be changing rapidly for plants and any of these changes can lead to dissociation between the cue and outcome, a potential evolutionary trap (Schuler and Orrock 2012). Plants respond to cues from their environments to optimize the initiation of important life processes (e.g., seed germination, bud formation, flower formation, fruit set, and leaf drop); the JDM framework provides a useful means to examine the success or failure of plant species exposed to novel climatic regimes. For example, plants might incorrectly judge that winter conditions are over and decide to initiate growth of young buds, leading to an increased likelihood that young buds will be damaged during a "false spring" when a warming event is followed by several more freezing events (Rigby and Porporato 2008, Augspurger 2013). In this scenario, the plant might correctly judge that winter is not over but nevertheless decide to initiate bud growth because strong competition with neighbors for light capture makes prioritizing bud growth a more profitable strategy given the certainty of competition and the probabilistic nature of false springs. An alternative scenario involves the plant correctly judging that winter is over, but opting to allocate resources to root growth (e.g., if a key soil-borne nutrient is limiting) instead of prioritizing bud growth. As these scenarios demonstrate, the same observable outcome (whether bud growth does or does not occur) can arise due to multiple combinations of judgments and decisions. Importantly, a failure to act need not represent a failure to accurately characterize the state of the world (i.e., that winter is really over), but can also result from the influence of costs and benefits unknown to the researcher, but known to the plant (and included in the decision process).

Increased opportunities for dispersal and changing biotic and abiotic conditions have resulted in a subset of species that are now considered invasive across geographic ranges that they did not occupy historically. Determining the characteristics that allow some plants to become invasive is an important research focus (e.g., van Kleunen et al. 2010, Richardson and Rejmanek 2011). The JDM framework may help us to understand and predict these biological invasions. For example, in seeking to understand which plants become invasive, the JDM framework emphasizes that plants must be capable of accurate judgment and appropriate decision making in the novel range. Failure to become invasive can arise because of an error in judgment (e.g., a plant is not capable of detecting cues important for success in the new environment) or because of poor decision making (the costs and benefits of responding to a cue in the novel environment are not appropriately weighted). False-positive errors can also contribute to failure to become invasive: if an invasive plant incorrectly identifies cues of harmless insects in the novel environment as a damaging herbivore, it may invoke costly and unnecessary defenses, akin to animals that exhibit costly anti-predator behaviors when they misidentify harmless animals as predators (Trimmer et al. 2017). Or, the plant may correctly identify herbivores in the novel environment, but incorrectly weight their potential for damage, again leading to an over-investment in defense relative to the amount of defense actually required.

Conclusions

Integrating plants within the judgment and decision-making framework should help clarify our thinking regarding how plants sense and respond to their environment, as well as help guide the design of exciting future experiments (summarized in Box 1). In focusing our attention on the components of behavior, the judgment and decision-making framework also highlights substantial gaps in our current knowledge. For example, although we appreciate that plants can sense many things about their environment, the degree to which plants can detect (and hence judge) cues from

Box 1. An overview of ecological and evolutionary questions that are informed or inspired by the application of the JDM framework to plants.

Differences in the actions of plants and animals

- How similar or different are the selective pressures on judgment and decision making faced by plants and animals?
- Are differences in judgment and decision making the result of information that they receive, the judgment process, their cognitive abilities, the costs and benefits of responding, and/or their abilities to respond?
- Do differences in tolerance to damage influence decisions?
- Can plants be used to test evolutionary theories regarding judgment and decision making because they are more tractable experimental systems than many animals?
- Are there differences in judgment and decision making when it is performed in a democratic fashion (e.g.,, plants, eusocial animals) vs. in situations where a central nervous system synthesizes information and chooses (e.g.,, individual animals)?
- Does the different temporal scale of judgment and decision making for plants and animals impose constraints on the evolution of plastic traits (variable strategies that result from judgment and decision making) and constitutive traits (invariant strategies that do not require judgment and decision making)?

Plant responses in existing interactions and environments

- Can Bayesian models be used to describe the accuracy of plant judgment?
- Can economic utility models describe costs and benefits of alternative plant decisions?
- What are the mechanisms by which herbivores and pathogens might influence or usurp plant judgment and decision making?
- How did current interactions between plants and their parasites (herbivores and pathogens) evolve in the context of judgment and decision making and what are possible evolutionary trajectories?
- Do mycorrhizae influence plant judgment and decision making and how might they be evolving?

Plant responses in novel interactions and environments

- Do matches in judgment and decision making (JDM match) between plant behavior and the novel environment predict invasiveness of introduced species?
- Do plants fail to become invasive because of mismatches in judgment, decision making or both?
- Does the JDM match predict which plants will be defended against novel herbivores?
- Why do some plants recognize novel herbivores while others do not?
- Can JDM predict which plants will successfully respond to climate change?
- Can JDM predict situations in which active management will be helpful to rescue at-risk species?

biotic sources is an active area of research (Karban 2015). Our appreciation of the ability of plants to perceive varied cues is rapidly growing (e.g., recent work suggests that plants can detect mating pheromones of their herbivores; Helms et al. 2013, 2017). Our understanding of decision making for plants is also rapidly growing but still quite incomplete. For example, it is not clear how plants integrate multiple sources of information from multiple attackers to arrive at an appropriate decision regarding how best to defend themselves. We feel that the judgment and decision-making framework may provide perspective to future studies of many pressing contemporary questions, such as the response of plants to changing climatic conditions, to introduced pathogens and herbivores, and to widespread habitat alteration.

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