Natural History Note

Applying Behavioral-Ecological Theory to Plant Defense: Light-Dependent Movement in *Mimosa pudica* Suggests a Trade-Off between Predation Risk and Energetic Reward

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ABSTRACT: Many animal species tolerate different amounts of predation risk based on environmental conditions and the individual's own condition, often accepting greater risk when energetically stressed. We studied the sensitive plant *Mimosa pudica* to see whether it too accepts greater risk of predation when less light energy is available. This plant displays a defensive behavior of rapidly folding its leaves when stimulated by touch, thereby decreasing visibility to herbivores. Averting herbivory involves a trade-off because leaf closure results in a reduction in light foraging. We manipulated the light environment of individual *M. pudica* plants and recorded the time it took a plant to reopen its leaves following stimulation as a measure of tolerance of predation risk. As predicted by theory, avoidance behavior was sustained longer under high light conditions than under more light-limited conditions. These findings suggest this species balances the risk and reward of antiherbivore behavior in relation to current environmental conditions and that behavioral-ecological theory is a useful framework for understanding plant responses to predators.

Keywords: plant behavioral ecology, predation-risk hypothesis, sensitive plant, light response.

Introduction

A common finding by behavioral ecologists is that animals will accept a greater risk of predation when energetically stressed than when energy is not limiting (Lima 1998). Such behaviors can be found in a variety of animal taxa ranging from sessile barnacles (Dill and Gillett 1991) to highly mobile birds (Koivula et al. 1995). Theory suggests there is a shifting balance between risks and rewards faced by individuals, such that at very low energy levels the costs associated with starvation risk are greater than the risk of predation (Lima 1998). Whether plants exhibit the same behavioral tendency to accept more predation risk when foraging for light under stressed (low light) conditions has not previously been tested.

The sensitive plant *Mimosa pudica* L. is fairly unique among plant species in that it is capable of rapid leaf movement. In response to physical disturbance, this species folds its leaves in a matter of seconds. The time required to reopen its leaves is highly variable, ranging from seconds to tens of minutes (J. F. Cahill Jr., personal observation). Recognition that the speed of reopening is quite variable is the basis for the research conducted here and leads to questions about the potential ecological and evolutionary costs and benefits of this leaf movement.

The rapid leaf folding action displayed by *M. pudica* is widely believed to reduce predation risk. The rapid movements may scare away herbivores, and the closed leaves decrease the visibility of the plant (Braam 2005) while also making morphological defenses such as thorns more visible (Eisner 1981). This unique defense tactic imposes costs through both the ATP required to reopen the leaflets (Fleurat-Lessard et al. 1997) and the opportunity cost associated with decreased ability to photosynthesize while the leaves are closed (Hoddinott 1977). Although animal defensive tactics often impose both energetic and opportunity costs, the dual costs of lost time and energy are rare among plants, or at least are rarely considered in theories of plant defensive strategies. Based upon the biology of this organism, there is reason to believe this plant may behave in a manner consistent with behavioral-ecological theory developed for animals (Lima 1998).

There is rapidly increasing evidence that plants exhibit a diversity of complex behaviors, including kin recognition (Dudley and File 2007), integration of information resulting in unique root foraging strategies (Cahill et al.

2010), and complex mechanisms of plant-plant and plant-animal communication (Karban 2008). Further, behavioral-ecological theory has been suggested as a powerful tool for understanding the potential costs and benefits of alternative plant strategies (McNickle et al. 2009). Understanding whether such a perspective would enhance understanding of this plant's defense behavior is the central goal of this study.

To understand *M. pudica*'s strategy for balancing the need for photosynthesis with the potential risk of predation, we measured the length of time it took plants to reopen their leaves following physical stimulation. Energetic stress was varied by performing these tests under a range of levels of photosynthetically active radiation (PAR). If *M. pudica* follows the energetic stress–predation risk hypothesis, then the plant should keep its leaves closed longer under high light conditions than under low light conditions, reducing predation risk. Importantly, this prediction is the opposite of what would be expected based purely on energetics, where it might be expected that plants in high light, having abundant energy available to them, would be able to more rapidly reopen their leaves.

Methods

Study Species

Mimosa pudica is a perennial shrub that, first identified in Brazil, now is a pantropical invasive weed (Francis 2010). Though native to the Southern Hemisphere, the rapid leaf movements have resulted in this species being regularly propagated in universities and colleges throughout the world for use in demonstrations of plant behavior.

The leaves are palmately compound and usually have two or four leaflets that are themselves pinnately compound. The folding action of the pinnules and petioles is caused by a rapid loss of turgor in epidermal and pulvinar cells and is hypothesized to be mediated by aquaporins (Braam 2005). The photosynthetic rate of *M. pudica* is reduced by up to 40% when leaves are closed (Hoddinott 1977), representing a significant opportunity cost associated with antipredator behavior.

We obtained six adult *M. pudica* individuals from the teaching collection in the University of Alberta phytotron. They were all approximately 1 year old, at their mature size, and in good health. Plants had been grown under ambient light in the greenhouse in 23-cm pots filled with a soil mixture of 20% black loam, 40% perlite, and 40% peat moss. Before our experiment, we pruned several of the most spindly branches to make the plants more manageable and to minimize the likelihood of their being accidentally bumped during testing.

Experimental Arenas and Tests

The experiment took place in a south-facing room in the greenhouses of the Department of Biological Sciences at the University of Alberta. Air temperature varied with ambient conditions but typically ranged between 20° and 22°C. On cloudy days, natural light was supplemented with artificial light (400-W sodium vapor lamps), although we avoided running trials on these days. Plants were fertilized and watered as needed to maintain plant health and growth.

A critical aspect of this study was to reduce the supply of resources (light) available to the plants prior to physical disturbance of the leaves. This was achieved by using combinations of shade cloth, supplemental lighting, and variations in time of day to create variations in PAR both below and above ambient levels within the greenhouse. Tests were conducted on 5 different days. Though we performed tests only on sunny days with minimal cloud cover, natural differences in PAR within and across days further enhanced the variation in resource supply received by the test plants.

On the morning of the day before testing, each plant was moved into position within the greenhouse. Plants were initially randomly assigned to either the high or low light regions of the greenhouse and were separated from each other so there would be no disturbance associated with brushing stems. While being moved into position, all the leaflets closed and petioles drooped. For the remainder of that day, the plants were not touched or stimulated in any way.

Testing began between 0900 and 1000 hours the day following plant placement. Stimulations occurred 1–1.5 h apart, and no more than four stimulations were performed on a plant on a given day. *Mimosa pudica* habituate to frequent disturbances (Applewhite 1972), but only if the leaflets are not given time to reopen between each stimulation. For this reason, we do not believe that habituation was a confounding factor in our experimental design. However, to account for the possibility of long-term habituation, we included the number of prior stimulations a plant received that day in our statistical model. Drying of the soil could also potentially reduce the rate of reopening, and this might be expected to be most pronounced under high light conditions. However, soils were saturated the day before the test, and there was no evidence of dehydration after a day's test. If such confounding effects did occur, we would expect rates of reopening to be slower later in the day than earlier, and thus we included time of day in our statistical model.

Using an AccuPAR light interception device (Decagon, Pullman, WA), PAR was measured directly above each plant immediately before stimulation. For each stimula-

tion, a healthy accessible leaflet was selected. The breadth of the longest pair of pinnules on the leaflet was measured tip to tip using digital callipers, being careful not to touch the plant in any way. Prestimulus leaflet breadth ranged from 12.8 to 32.3 mm among leaves, with a mean of 22.0 (SD 4.3). Since these measures could not be taken while holding the leaf because it would have closed, we recognize that some degree of measurement error is introduced.

The leaf being monitored was then stimulated at the base of the secondary pulvinus by a finger prod of sufficient force to cause all the pinnules of that leaflet to close. The plant's pot was then shaken gently until all of the other leaflets closed and petioles drooped. These dual stimulations were used because of the difficulty of handling a plant that is sensitive to touch. The direct finger prod on the focal leaf ensured that that particular leaf received a force of sufficient strength to close all of its pinnules. That force would occasionally, but not always, cause the closure of additional leaves that were not directly prodded. Because the number of leaves that closed in response to a single prod and the locations of these leaves varied among trials, we chose to ensure a standard level of disturbance by shaking the pots of all plants. This forced the closure of all leaves in all trials, though not all pinnules of all leaves would droop. We did not use data from trials when we accidentally bumped the plant. In total, we had 8–20 sets of measurements (described below) for each plant.

Each minute after stimulation of the focal leaf, the width of the leaflet at the longest pair of pinnules was remeasured until it reopened to within 1.5 mm of its original breadth. We used this reduced target as our measure for 100% reopened because of occasional overestimates of prestimulus leaf breadth due to the error associated with measuring leaves without being able to touch them. From these data we then calculated the time it took a plant to reopen its leaves to 75% of its original breadth.

Following a day's testing, plants were returned to ambient light conditions until weather permitted an additional day of testing. We then randomly selected the plants for placement in the greenhouse on the next day of testing.

Statistical Analyses

We conducted a general linear mixed-model analysis in SPSS version 18.0 (SPSS 2009). Time to reopen (75%) was normally distributed and served as the response variable. Because of multiple measures taken on individual plants, we included plant as a random effect; PAR at the time of stimulation, time of day, and number of prior stimulations served as three fixed effects.

We had concerns about the accuracy of the data related to 100% reopening, and thus only the 75% reopening data were used in our final analysis. More specifically, we found

that some plants would reopen their leaves to greater than 75% but not to 100% within a reasonable time frame, resulting in many outliers in the latter data set. Furthermore, we reasoned that once the leaflets were 75% recovered, the plant would probably be apparent to herbivores, and its photosynthetic rate would be only slightly reduced. Conclusions from the analysis of the 100% data set are nearly identical to those based on the 75% data set.

Results

Mimosa pudica displayed substantial variation in the time it took to reopen leaves following a disturbance, ranging from approximately 3 to 13 min. There was a strong positive relationship between PAR and time to reopen leaves (fig. 1; table 1). This result indicates that plants currently under more stressful conditions (low light) exposed themselves to greater predation risk than plants currently under less stressful conditions. Neither time of day nor the number of previous stimulations that day affected the time required for the leaves to reopen (table 1).
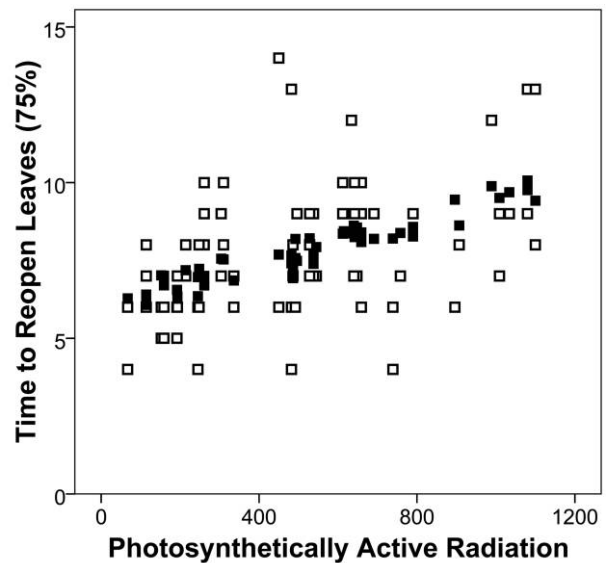

Figure 1: Length of time (min) following physical stimulation required for leaflets to reopen to 75% of their original breadth as a function of photosynthetically active radiation (μmol s^{-1} m^{-2}). Open squares are the raw data; filled squares are the predicted values from the mixed model that included additional fixed and random factors. The additional model factors explained some of the variation in the time to reopen and, thus, the improved (though not perfectly linear) fit.

Discussion

Closing leaves in response to physical stimuli presents several energetic challenges for *Mimosa pudica*. A simple energetic hypothesis would expect recovery to be fastest when light levels are highest, due to the ATP-dependent steps required in reopening leaves. Conversely, energetic considerations may lead to the expectation that leaves under low light conditions would be less tolerant of further reductions in photosynthetic capacity and thus would rapidly reopen their leaves. However, the potential cost of rapid recovery is increased predation risk, and thus, there is a trade-off between foraging for light and predation risk. We found that plants in low light reopened their leaves faster than plants under high light conditions (fig. 1), consistent with the prediction that more energetically stressed individuals will tolerate greater predation risk than less-stressed individuals (Lima 1998).

This behavioral-ecological approach to understanding plant defense strategies is a departure from the traditional approach used to understand plant-herbivore interactions. For example, the compensatory continuum hypothesis (Maschinski and Whitham 1989) and the limiting resource model (Wise and Abrahamson 2005) make specific predictions about the allocation of chemical defenses as a function of resource conditions, but neither explicitly addresses behavioral responses. Karban (2008) has suggested that many aspects of plant biology could be viewed in a behavioral context, including plant defense. The data we present here (fig. 1) support such a contention and highlight the need to reevaluate the factors typically included in models of plant defense allocation. For example, no existing plant defense model includes the opportunity costs associated with time spent avoiding predators versus foraging (as is common among animals); instead, existing theory focuses on nutritive and energetic costs. It is perhaps not surprising, then, that an animal-based theory provides a potential explanation for the observed patterns. We suggest, however, that this is just a first step in this direction, and future use of animal-based models needs to be adjusted for the unique aspects of plant biology (e.g., McNickle et al. 2009).

It has been suggested that the leaf folding behavior of *M. pudica* has benefits for the plant other than deterring herbivores. Wallace et al. (1987) tested the hypothesis that leaf folding was a mechanism for reducing foliar nutrient loss in response to rainfall (one source of physical stimulation). By anesthetizing the plants, the researchers were able to prevent leaf closure, though they found no evidence of foliar nutrient leaching in either the experimental or the control plant groups. Eisner (1981) found that leaf folding increased the visibility of thorns of another sensitive plant, *Schrankia microphylla*. He suggests that by

Table 1: Results from a general linear mixed model

	df	F	P
Photosynthetically active radiation	1, 74	23.07	<.001
Time of day	1, 73	.38	.538
Number of prior stimulations	1, 73	2.34	.126

Note: Time to reopen leaves to 75% original breadth served as the response variable. Photosynthetically active radiation before stimulation, time of day, and the number of prior stimulations served as fixed effects. Due to multiple measures taken on individual plants ($n = 6$), plant identity was included as a random factor.

folding its leaves, the plant may increase the effectiveness of its mechanical defenses in deterring herbivory. If Eisner's ideas are also applicable to *Mimosa*, it still does not provide an explanation for the light-dependent behavioral responses we observed. Instead, it would raise a new question: Why would the plant expose thorns longer under high light conditions than under low light conditions? We suggest that our behavioral interpretation remains plausible and consistent with the idea that resource stress causes individuals to accept greater predation risk.

We recognize that there exist other potential non-defense-related explanations for the leaf closure behavior exhibited by *M. pudica*, some of which may be consistent with the light-dependent responses we observed. For example, leaf closure reduces photosynthesis (Hoddinott 1977) and, thus, transpiration rates. There may be adaptive value in delayed leaf opening under high light conditions as a means of water conservation. However, to the best of our knowledge, there are no data directly testing the influence of soil moisture on leaf closure behavior in this species. Further, this was a greenhouse experiment of relatively short duration, and plants were watered regularly. Nonetheless, experimental tests of alternative explanations are warranted.

Mimosa pudica exhibited a behavioral strategy consistent with other organisms that use movement as a means of reducing the risk of predation. When resources were abundant, there was prolonged avoidance of predation risk, while, when grown under limited light conditions, there was increased tolerance to predation risk. In animals, the economics of such a response have been examined in detail (Dill and Gillett 1991; Dill and Fraser 1997), and we suggest that this theory should be expanded to include plants. This study joins many recent studies indicating that a behavioral-ecological perspective can provide novel insights into plant biology and plant-herbivore interactions.

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Natural History Editor: Craig W. Benkman

Left, *Mimosa pudica* leaf at its resting position, with pinnules fully exposed; *right*, the same leaf a few seconds after being prodded, with its pinnules folded in. Photographs by Evelyn Jensen.