INFLUENCE OF LIGHT AVAILABILITY ON DELAYED GREENING STRATEGY IN *WELFIA GEORGII*

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Abstract: In tropical forests, to deter herbivores and reduce losses to herbivory in young leaves, some plants delay the greening of leaves with chlorophyll until chemical and structural defenses have developed. We hypothesized that *Welfia georgii* would adjust delayed greening strategy depending on light availability. We predicted that the proportion of *W. georgii* individuals exhibiting delayed greening would decrease with canopy openness, because the cost of decreased photosynthesis resulting from delayed greening (i.e., in an environment in which light is highly available) would be greater than the benefit of decreased herbivory. Contrary to this hypothesis, we found that the proportion of individuals with delayed greening increased with canopy openness. We propose that this may be due either to light saturation of *W. georgii* under open canopy or to higher herbivory pressure in tree-fall gaps. We also found that young leaves without delayed greening had more damage from herbivory than young leaves with delayed greening, suggesting that this defense is effective against herbivores.

Key Words: canopy openness, herbivory, light saturation, photosynthesis, tree-fall gap, tropical rain forest, understory

INTRODUCTION

Herbivory in tropical forests occurs mostly on young, expanding leaves (Coley and Aide 1991, Coley and Kursar 1996). Delayed greening is a strategy that reduces the resources lost to herbivory by postponing production of valuable chlorophyll in young leaves until after chemical and structural defenses have developed (Coley and Kursar 1996). Consequently, leaves with delayed greening are less nutritious and less preferred by herbivores (Coley and Kursar 1996). While delayed greening helps protect young leaves against herbivory, there is a high cost associated with allocating resources to a leaf that does not fix carbon through photosynthesis.

Welfia georgii, an abundant palm at La Selva Biological Station, in the Atlantic lowlands of Costa Rica, exhibits delayed greening. It can germinate and develop slowly in low light, but grows rapidly when a light gap is created after a tree or branch fall (Vandermeer 1983). We hypothesized that *W. georgii* would adjust its delayed greening strategy based on light availability. We expected that, for *W. georgii* in high light conditions, the cost of decreased photosynthesis resulting from delayed greening would be greater than the benefit of decreased herbivory, because *W. georgii* can take advantage of ample light resources (Fig. 1). We predicted that *W. georgii* under high canopy cover would exhibit more delayed greening than those under low canopy cover. We also predicted that there would be less herbivory on

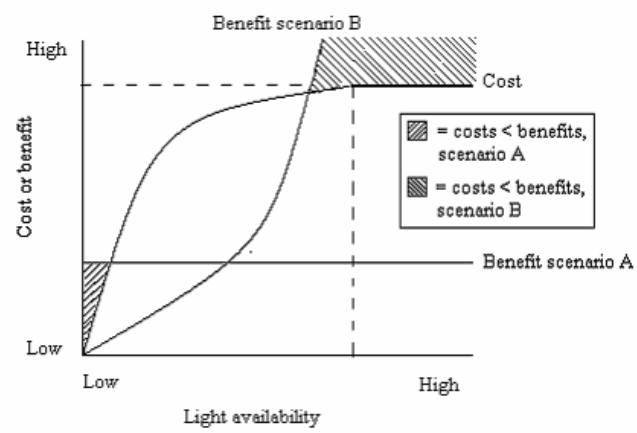

Figure 1. A theoretical model of costs and benefits of delayed greening with changes in light availability. All axes are in fitness units. Dashed lines represent the light saturation point of leaves. "Cost" represents the cost of delayed greening in terms of lost photosynthesis opportunity. "Benefit scenario A" represents the benefit of delayed greening in terms of herbivory prevention, when this benefit is constant over different light environments. In this case, delayed greening should occur only at low light availability, which was consistent with our prediction, but inconsistent with our findings. "Benefit scenario B" represents the benefit of delayed greening in terms of herbivory prevention, when this benefit increases exponentially with light availability. In this case, delayed greening should occur at high light availability, which is consistent with our findings. Examining how these costs and benefits change with light availability is crucial to a full understanding of delayed greening response in *Welfia georgii*.

young leaves with delayed greening than on those without delayed greening.

METHODS

On 13 and 14 February 2005, we sampled 137 *Welfia georgii* along the Camino Experimental Sur from 10 to 772 m from the trail head at La Selva Biological Station, Costa Rica (excluding the restricted access plot from 450 to 550 m). We measured *W. georgii* height, canopy openness, leaf maturity, and percent herbivory for all individuals within 5 m of the trail. We also assessed whether each plant exhibited delayed greening, defined as possessing a young leaf with any red coloration.

We identified the youngest leaf of each plant, which had a central position relative to other leaves. Because all leaves eventually turn green, we wanted to ensure that the color of leaves reflected their delayed greening strategy, not their age (i.e., that we were not sampling leaves that once had delayed greening, but had since matured). To do so, we rated the maturity of the youngest leaf on a scale from 0 (unopened leaf) to 5 (nearly mature) by comparing degree of folding, color, and texture to mature leaves on the same plant. According to this scale, younger leaves had more folding, lighter coloration (red or green), and less toughness than more mature leaves.

We chose only plants shorter than 4 m possessing one young leaf (defined as less than or equal to five on this scale). We excluded plants with ambiguous red coloration at the base of the leaflets. We measured each plant's height with a meter stick and assessed openness of the canopy above each plant with a spherical densiometer. We estimated the percent of young leaf area removed by herbivores by averaging the visual estimates of three observers.

All statistical analyses were performed using JMP 4.0.0. Data met or were transformed to meet all assumptions of parametric tests. Percent herbivory was normalized by an arcsine transformation.

RESULTS

Of the 137 *W. georgii* sampled, 66 exhibited delayed greening in their youngest leaf and 71 did not. Maturity of the youngest leaves on each plant did not differ between delayed greening and non-delayed greening plants (Wald test for ordinal logistic fit, $\chi^2 = 1.36$, df = 1, P = 0.24), and was not related to canopy openness (Wald test for ordinal logistic fit, $\chi^2 = 0.004$, df = 1, P = 0.95). The proportion of *W. georgii* exhibiting delayed greening increased with canopy openness, although this result was not significant (logistic regression, $\chi^2 = 2.35$, df = 1, P = 0.13; Fig. 2).

Percent herbivory on young leaves was greater for non-delayed greening plants (2.87 ± 0.52%) than for delayed greening plants (0.58 ± 0.54%; F = 9.84, df = 106, P = 0.002; Fig. 3). However, we found no relationship between percent herbivory and canopy openness ($r^2 = 0.003$, df = 135, P = 0.51).

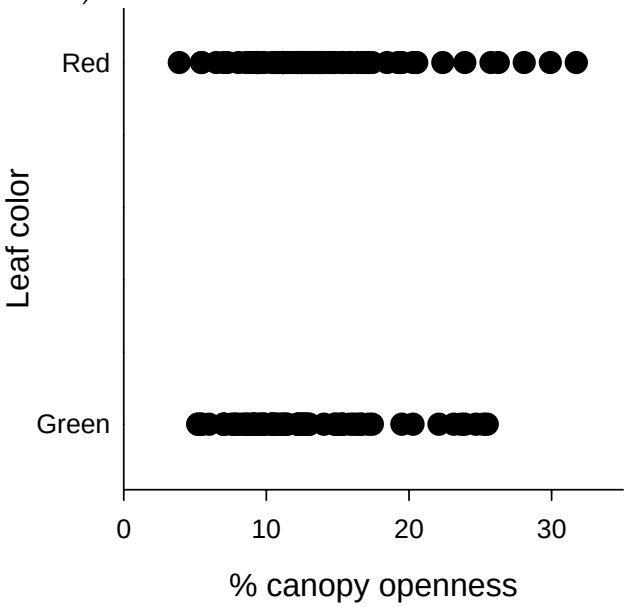

Figure 2. The proportion of *Welfia georgii* exhibiting delayed greening (i.e., red coloration) increased with canopy openness (n = 137).

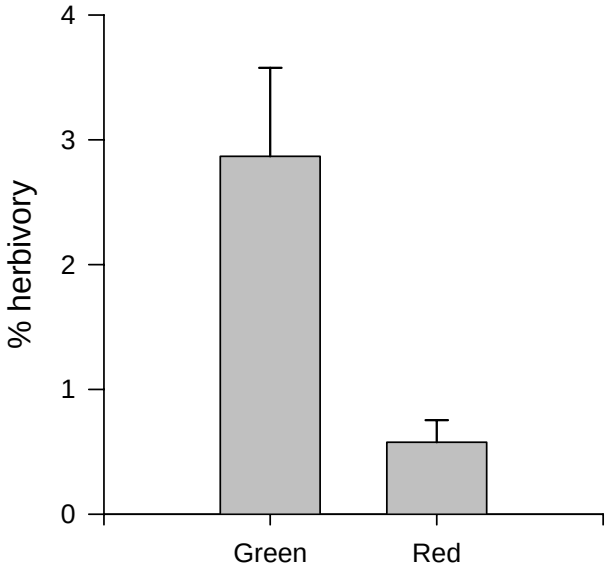

Figure 3. More herbivory was observed on young leaves of *Welfia georgii* without delayed greening (youngest leaf was green) than on young leaves of plants with delayed greening (youngest leaf was red).

DISCUSSION

We found no difference in maturity between young leaves exhibiting delayed greening and those lacking this defense. This suggests that delayed greening in *W. georgii* is a plastic response, rather than a fixed stage in leaf development. We observed nearly as many newly unfolding completely green leaves as red leaves, which supports this conclusion. Our finding that leaves with delayed greening had less herbivory than green leaves suggests that delayed greening is effective in preventing herbivory. The result that percent herbivory increases with leaf maturity is to be expected, since older leaves have accumulated herbivory damage over a longer period of time than younger leaves.

Contrary to our hypothesis that delayed greening would be more costly for plants in gaps than in the understory, we

found that the proportion of *W. georgii* with delayed greening increased with canopy openness. This could be due to differences in light availability. Plants in gaps may be light saturated, so that maximum photosynthesis occurs even if plants only capture a fraction of available light. Possession of non-photosynthetic tissue (i.e., leaves with delayed greening) is, therefore, not as costly to the overall rate of photosynthesis for a plant. Plants in the shaded understory receive less light, often in the form of transitory sunflecks, and may need to capture as much of this light as possible to maximize photosynthesis.

In minor light gaps *W. georgii* grows quickly and competes well, but in the shaded understory it grows slowly (Vandermeer 1983). This indicates that *W. georgii* leaves probably have an intermediate light saturation point. In gaps, *W. georgii* may reach its saturation point. In this case, photosynthesis would be occurring at the maximum rate, and non-photosynthetic tissue would be less costly.

An alternative explanation for the positive relationship between canopy openness and delayed greening is that pressure from herbivores may be higher in gaps. Gaps contain faster-growing, poorly defended, and more palatable plants than the understory, and may attract more insect herbivores (Coley and Kursar 1996). Higher abundance of herbivores would increase the advantage of delayed greening (i.e., Benefit scenario B in Fig. 1), which is consistent with our finding that leaves with delayed greening have less herbivory. Although we found no relationship between herbivory levels on young leaves of *W. georgii* and canopy openness, it is possible that our measurements of herbivory do not reflect relative herbivore abundances in the two habitats.

We suggest that, based on the natural history of *W. georgii*, light availability and its effect on herbivory may drive the trend towards increased delayed greening in gaps. Further studies could compare the abundance of herbivores on *W. georgii* in gaps and in the understory to determine if the benefits of delayed greening in terms of herbivory prevention change with light availability (see Fig. 1). A study to determine the light saturation point of *W. georgii* would provide information about the potential for *W. georgii* saturation in gaps.

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EFFECT OF FOOD RESOURCES ON THE ABUNDANCE OF *DENDROBATES PUMILIO* TERRITORIES

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Abstract: The poison dart frog *Dendrobates pumilio* defends reproductive resources in territories year-round (Donnelly 1989). We hypothesized that *D. pumilio* territory abundance was also related to the abundance of food resources. We predicted that there would be fewer territories in areas with lower insect abundance than in areas with higher insect abundance. We measured insect and frog territory abundances in two forest types. Secondary forests were found to have higher insect and frog abundances than primary forests, and *D. pumilio* territory abundance increased with increasing small insect abundance. We suggest that the density and location of *D. pumilio* territories may be determined by food abundance in addition to reproductive resources.

Key Words: food availability, frog density, strawberry poison dart frog

INTRODUCTION

The strawberry poison dart frog, *Dendrobates pumilio*, is commonly found in tropical lowland forests. They maintain territories year-round by calling, and the number of calling frogs is indicative of the number of territories in an area (Savage 2002). It has been proposed that the main purpose of these territories is to secure reproductive resources such as bromeliad tanks and leaf litter (Donnelly 1989). Because *D. pumilio* require high abundance of small insects (< 3 mm) to meet their metabolic needs (Savage 2002), we hypothesized that *D. pumilio* territories might be