Biology:

Influence of Light Availability on Delayed Greening Strategy in Welfia Georgii

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Abstract: To deter herbivores and reduce losses to herbivory, some tropical plants delay the production of chlorophyll (i.e., greening) in young leaves until chemical and structural defenses have developed. We hypothesized that the palm Welfia georgii would adjust its 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, in an environment in which light is highly available, the cost of decreased photosynthetic rate 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. 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.

Herbivory in tropical forests occurs mostly on young, expanding leaves (1,2). 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 (3). Consequently, leaves with delayed greening are less nutritious, less preferred by herbivores, and appear red instead of green (4). 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, Costa Rica, is one type of plant that 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 (5). 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 young leaves with delayed greening than on those without delayed greening.

**Methods**

On 13 and 14 February 2005, we sampled 137 *Weltia georgii* along the Camino Experimental Surf from 10 to 772 meters from the trail head at La Selva Biological Station, Costa Rica (excluding a restricted access plot from 450 to 550 meters). We measured canopy openness, *W. georgii* height, leaf maturity, and percent herbivory for all individuals within five meters of the trail. We also assessed whether each plant exhibited delayed greening, defined as possessing red coloration in the youngest leaf. In *W. georgii*, the youngest leaf is the most central.

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 exhibited 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 our maturity scale). Plants with ambiguous red coloration at the base of the leaflets were excluded. We measured each plant’s height with a meter stick and assessed openness of the canopy above each plant using a spherical densiometer. The percent of young leaf area removed by herbivores was assessed 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 the 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, $X^2 = 1.36$, df = 1, $p = 0.24$), and was not related to canopy openness (Wald test for ordinal logistic fit, $X^2 = 0.004$, 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, $X^2 = 2.35$, df = 1, $p = 0.13$; Fig. 2).

Percent herbivory on young leaves was greater for non-delayed greening plants ($2.87 \pm 0.52\%$) than for delayed greening plants ($0.58 \pm 0.54\%$; 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, $p = 0.51$).

**Discussion**

We found no difference in maturity between young leaves exhibiting delayed greening and those lacking this defense. This confirms that delayed greening in *W. georgii* is a plastic response, rather than a fixed stage in
leaf development. We observed many newly unfolding green 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.

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), therefore, may not be as costly to the overall rate of photosynthesis for a plant in high light conditions as it is for a plant in low light conditions. 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. *W. georgii* grows quickly and competes well in minor light gaps, but grows slowly in the shaded understory (6). This palm may therefore have an intermediate light saturation point, suggesting that light levels in large tree-fall gaps could saturate the plant's photosynthetic capacity.

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, more poorly defended, and more palatable plants than the understory, and therefore may attract more insect herbivores (7). Higher abundance of herbivores would increase the advantage of delayed greening in gaps (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.

Based on the natural history of *W. georgii*, we suggest that light availability and its effect on herbivory may drive the positive relation between incidence of delayed greening and light availability. Further studies could compare the abundance of herbivores in gaps and in the understory to determine if herbivory pressure changes with light availability (see Fig. 1). A study to determine the light saturation point of *W. georgii* would provide information about the potential for saturation in gaps.

REFERENCES