The effects of light environment and herbivory on delayed greening of tropical forest leaves

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Abstract: Most herbivory occurs on expanding leaves. If a plant loses more resources to herbivory than it gains from photosynthesis in its expanding leaves, delaying chlorophyll input to those leaves may benefit the plant. We hypothesized that low light levels and high herbivory would correspond to higher amounts of delayed greening in leaves of tropical montane forest. Therefore, we predicted that plants in the shaded understory, where herbivory is presumably high, would display delayed greening more frequently than those in a nearby open area. We sampled transects of both open and shaded environments and counted both abundance and number of morphotypes of plants that displayed delayed greening. We found that there was higher herbivory and more delayed greening on leaves growing in the shade than in more open areas. Our results suggest that light levels and herbivory do influence the frequency of delayed greening of leaves in tropical forests.

Key Words: photosynthesis, shade leaves

Introduction

Up to 70% of all herbivory can occur on expanding leaves (Kursar and Coley 1992), since older, more fully expanded leaves are tougher and usually have chemical defenses that decrease the risk of loss to herbivory. If a plant loses more resources to herbivory than it gains from photosynthesis in its expanding leaves, as in a low light or high herbivory environment, it may be beneficial for the plant to delay the input of chlorophyll and rubisco until full leaf expansion has occurred (Kursar and Coley 1992). Conversely, in high light conditions with low herbivory, the sacrifice in photosynthesis associated with delayed greening may be unnecessary.

We hypothesized that both light environment and level of herbivory would affect the amount of delayed greening. We predicted higher abundance of delayed greening morphotypes and individuals in shaded than in open environments, due to lower capacity for photosynthesis and therefore decreased loss from unproductive, delayed-green leaves. We also predicted a positive correlation between herbivory level and delayed greening frequency, since loss of productive tissue to herbivory is minimized with delayed-green leaves, which would be more necessary at higher herbivory levels.

Methods

We haphazardly selected 17 transects along the lower portions of the eastern end of the loop trail near Estación Cuericí, Costa Rica, of which 11 transects were shaded by forest canopy and six were outside the forest in a neighboring old field, which was regenerating and exposed to direct sunlight. Each transect was 5 m long and 1 m wide. Within each transect we counted the number of morphotypes and abundance of plants with expanding leaves between 0.5 m and 2.5 m off the ground, excluding grasses. Morphotypes for which at least one individual was found to have delayed greening leaves were classified as exhibiting delayed-greening. The frequency of delayed and non-delayed greening morphotypes were compared between shade and sun using a t-test. The frequency of delayed and non-delayed greening individual plants were compared between shade and sun using chi-square analysis. We collected one sample of each morphotype from each transect to maintain consistency in morphotype identification among transects. We estimated percentage of herbivory on five haphazardly selected leaves from the first individual of each morphotype encountered in each transect, and compared the means between environments using Welch's ANOVA.

Prior to sampling, we practiced estimating percentage of herbivory until our estimates consistently matched measured percentages (correctly estimating 10 out of 10 practice leaves).

Results

There were significantly more delayed-greening individuals in the shaded than in the open environment ($\chi^2 = 16.65$, $P < 0.0001$; Table 1). There was no significant difference in proportion of delayed greening morphotypes between open and shaded environments ($t = -1.11$, $df = 15$, $P = 0.29$), though the number of delayed greening morphotypes was higher in the shade (Table 1). There was a higher percentage of herbivory in the shaded than in the open environment (Welch's ANOVA, $F = 13.06$, $df = 1$, $P < 0.0005$; Fig. 1). A morphotype-area curve for each environment showed that our sampling of the sun environment was more representative of all morphotypes present than our sampling effort in the shade (Fig. 2).

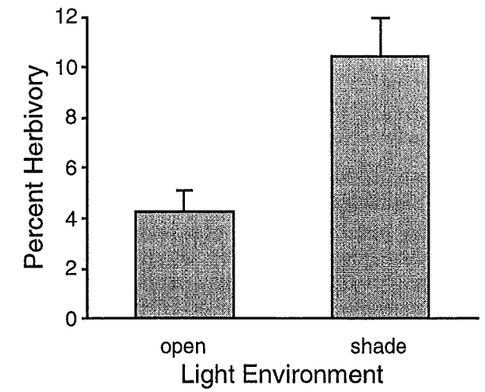

Fig. 1. Mean percent herbivory (± 1 SE) in shaded and open environments, as estimated on five leaves of all morphotypes sampled in each transect (open n = 35, shaded n = 50). (Cerro Cuerici, Costa Rica)

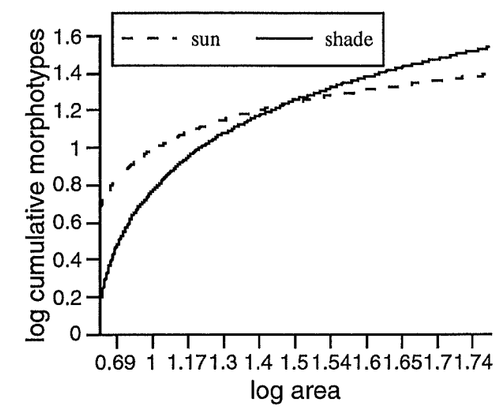

Fig. 2. Morphotype-area curve (log number of recognizable morphotypes) in open (n = 6) and shade (n = 11) environments (open, $r^2 = 0.9$; shade, $r^2 = 0.98$, log fit).

Discussion

The correlation of both lower light and higher herbivory with a higher number of delayed greening individuals is consistent with the theory that one or both of these factors favor delayed greening in plants. Delayed greening is one strategy by which certain shade-tolerant plants may cope with an environment where light resources are limited and herbivory is high. The relative contribution of these two factors, however, is difficult to determine, and merits further study.

The difference between open and shaded areas in the number of delayed greening morphotypes may increase with further sampling. The morphotype-area curves (Fig. 2) suggest that further sampling would detect more morphotypes in the shaded environment, some of which might display delayed greening. Additionally, as compared to the study conducted by Kursar and Coley (1992), the shaded environment at Cuerici had relatively high light and low overall herbivory (see Kursar and Coley 1992). We expect that a comparable study including a darker low light environment and/or higher herbivory would result in a more dramatic difference in delayed greening between environments.

Literature Cited

Kursar, T. A., and P. D. Coley. 1992. Delayed development of the photosynthetic apparatus in tropical rain-forest species. Functional Ecology 6: 411-422.