Effects of delayed greening on tissue loss to herbivory

R. M. BRAYCE, A. E. HANKE, AND A. E. SANTORO

Abstract. Delayed greening , the delayed production of chlorophyll in newly flushed leaves reduces N content, and may thus reduce palatability. We predicted that delayed greening species would have lower herbivore damage than non-delayed greening plants. However, we found no difference in the percent herbivore damage between delayed greening and non-delayed greening plants. Thus, delayed greening does not appear to deter herbivory, but may reduce nitrogen losses to herbivores.

Key Words: anti-herbivore defense, abscised leaves.

INTRODUCTION

Delayed greening, the delayed production of photosynthetic material in newly flushed leaves, is common in tropical forest understory species and has been proposed as a mechanism reducing losses to herbivores (Kursar and Coley, 1992). Herbivory is usually high on immature leaves because they lack the lignin that makes older leaves unpalatable (Coley, 1983). Delaying input of nitrogen-containing compounds into developing leaves may (i) reduce leaf nutritional quality, tending to reduce herbivore consumption and (ii) reduce the nutrient loss for tissue that is consumed.

We tested the first of these hypothesized effects, i.e. the effectiveness of delayed greening in reducing herbivore damage on young leaves. Specifically, we predicted that herbivory on both immature and mature leaves would be lower for delayed greening plants than for those with normal leaf development. We also predicted leaf abscission would be more common in delayed greening plants; since fewer resources have been invested in immature leaves, they may be more likely to be shed after damage than leaves on non-delayed greening species.

METHODS

We surveyed understory plants within 2 m of the main trail from La Estación Biológica to the Great Divide, on January 22 and 23, 1999 in the Monteverde cloud forest of Costa Rica. We selected the first 8 delayed greening plant morphotypes encountered, then sampled them in approximately equal abundances, for a total of 53 individual plants. Percent herbivore damage was estimated on immature leaves at the first 4 nodes, and on the first 3 lignified, mature leaves of the apical branch. On these first 7 nodes, we recorded whether the leaf was present or not.

For each delayed greening plant sampled, a "nearest neighbor" non-delayed greening plant species of similar size was selected. Percent herbivore damage was measured on the first 3 unlignified, immature leaves, and on the first 3 lignified, mature leaves of the apical branch. The number of leaves abscised from these six nodes was recorded.

RESULTS

For both delayed greening and non-delayed greening plant species, the majority (>70%) of individual immature and mature leaves had experienced no herbivory (Fig 1).

There was no significant difference in herbivore damage between the immature leaves of delayed greening (6.3% ± 2.4 (mean ± S.E.)) and non-delayed greening species (1.9 % ± 0.89; Fig 2). Nor was mean percent herbivore damage on the first three extant mature leaves on delayed greening plants (12.8 % ± 1.98) significantly different from that on non-delayed greening plants (9.15 % ± 1.6; Fig.2).

Herbivores had removed significantly more tissue from extant mature leaves than from immature leaves, for both delayed greening plant species (Kruskal-Wallis: ChiSquare= 45.8, df=1, P<0.001), and non-delayed greening plant species (Kruskal-Wallis: ChiSquare= 42.4, df=1, P<0.001).

Mean number of abscised leaves on the first 7 nodes for delayed greening species was similar (0.28 ± 0.09) to that on the first 6 nodes for non-delayed greening species (0.38 ± 0.1; Kruskal-Wallis: ChiSquare= 0.49, df=1, P=0.48).

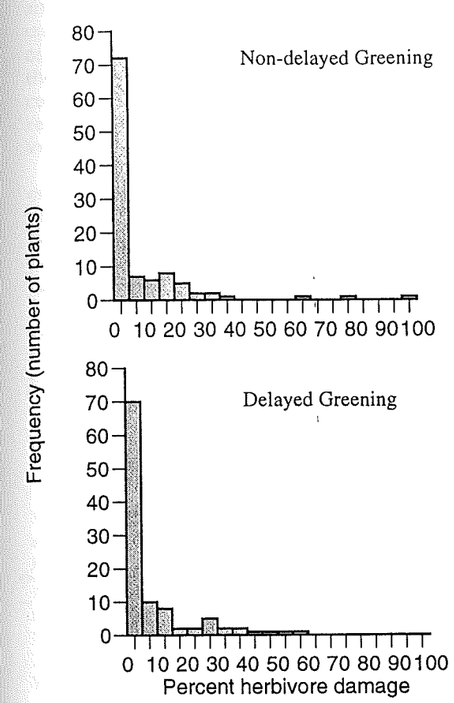

Fig. 1. Percent of leaf loss to herbivore damage on immature and mature leaves for non-delayed greening (n=53 individuals of 8 morphotyeps) and delayed greening (n=53 individuals) plants at Estation Biologica, Monteverde, Costa Rica.

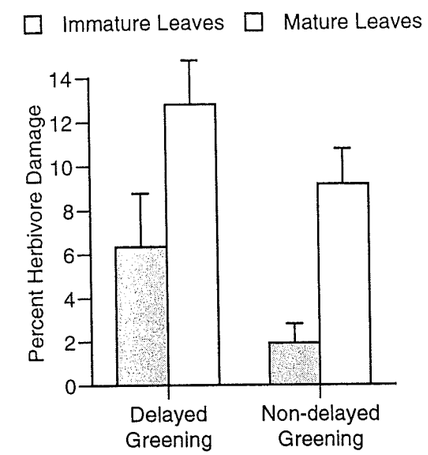

Fig. 2. Mean percent herbivore damage on extant leaves for delayed greening plants(n=53 individuals of 8 morphotypes) and non-delayed greening plants (n=53 individuals) at Monteverde, Costa Rica (means± S.E.). There was no significant difference in hervivore damage among immature leaves (Kruskal-Wallis: X^2=45.84, df=1, P=0.46), and mature leaves (Kruskal-Wallis:X^2=1.99, df=1, P=0.16).

DISCUSSION

Contrary to our expectations and those of Kursar & Coley (1992), we found no evidence that delayed greening deters herbivory; delayed greening and non-delayed greening plant species had similar levels of herbivore damage. However, the investment lost may be less for delayed greening than for non-delayed greening plants, because their immature leaves have less chlorophyll, nitrogen, and rubisco than the immature leaves of non-delayed greening plants.

The low incidence of abscission on both delayed and non-delayed greening species suggests that herbivore damage is rarely severe enough to eliminate the net energy gain from extant leaves. Although delayed greening does not deter herbivory, it may impart a net advantage over non-delayed greening plants if the reduction in nutrient loss to herbivory more than compensates for the reduced photosynthesis in leaves with delayed greening.

LITERATURE CITED

Coley, P. D. 1983. Herbivory and defensive characteristics of tree species in a lowland tropical forest. *Ecological Monographs*, 53(2), 209-233.

Kursar, T. A. and Phyllis D. Coley. 1992. Delayed greening in tropical leaves: An anti-herbivore defense? *Biotropica*, 24 (2b), 256-262.