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## The effects of rapid leaf expansion on the growth and survivorship of a lepidopteran herbivore

T. Mitchell Aide and E. C. Londoño

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*Gustavia superba*, a common understory tropical tree in the young forest of Barro Colorado Island, Panamá, produces leaves synchronously and has very rapid leaf expansion. Rapid leaf expansion followed by a decrease in leaf “quality” contribute to larval mortality of a major herbivore, *Entheus priassus*. Most larval mortality occurs during the first and second instars and appears to be directly related to leaf age at the time of hatching. Larvae that hatch on expanding leaves have a higher probability of surviving than larvae that hatch on fully expanded leaves. Because of the rapid leaf expansion, ovipositing *E. priassus* females have only a few days to locate suitable host leaves. We believe that rapid leaf expansion in *G. superba* acts as a defense by minimizing the time the leaf is acceptable for oviposition due to the rapid decline in leaf quality after the completion of leaf expansion. A possible cost of rapid leaf expansion is high levels of nitrogen in the young leaves, which may make these leaves more palatable to a greater range of herbivores.

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### Introduction

Plants have evolved an array of chemical (Harborne 1977, Zucker 1983) and structural defenses (Rathcke and Poole 1975, Shapiro 1981, Coley 1983) which have been demonstrated to minimize damage from insect herbivores. In response to these plant defenses, insects have evolved the ability to detect more palatable leaves (Feeny 1970), to detoxify many chemical defenses (Brattsten 1979) and in some cases, to sequester these compounds for use in their own defense (Brower 1969).

A review of plant/herbivore studies has shown, for most plant species, that young leaves are damaged at a higher rate than are mature leaves (Feeny 1970, Milton 1979, Coley 1983, Coley and Aide 1989). Even though some species have higher levels of chemical defenses in the young leaves, it appears that the benefits of feeding on these nutrient-rich tender leaves often outweigh the costs of processing the defenses (Scriber and Slansky 1981). If herbivores have evolved mech-

anisms to detoxify chemical or circumvent structural defenses, there should be a selective advantage to those plants which evolve novel types of defenses. A possible means of defense that has received little attention is the timing of leaf production. It has been suggested that synchronously flushing species may minimize damage to new leaves by satiating herbivores (Feeny 1970, McKey 1979, Coley 1983, Lieberman and Lieberman 1984, Aide 1988). At the individual level, rapid and synchronous leaf expansion may also act to deter feeding on young leaves by minimizing the time young vulnerable leaves are available to herbivores (Crawley 1983, McKey, in press).

We describe the interactions between *Gustavia superba* (H.B.K.) Berg (Lecythidaceae), a tropical tree, and *Entheus priassus* L. (Hesperiidae), a common herbivore of the young leaves, and suggest that rapid leaf expansion reduces herbivore damage to young leaves.

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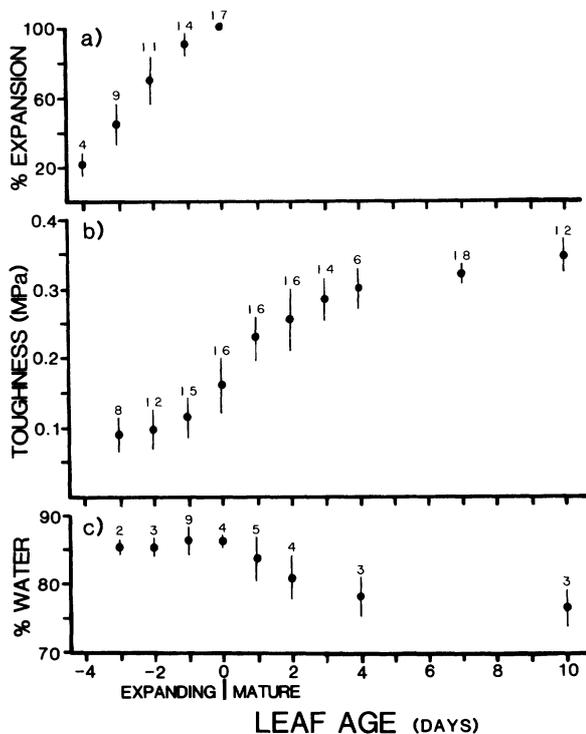


Fig. 1a–c. Mean  $\pm$  1 SD of a leaf characteristics of expanding and young mature leaves of *G. superba*. (a) leaf expansion rate (all leaves were full size on “day 0”), (b) leaf toughness (Mega-Pascals [MPa]), (c) percent water content. Numbers above the error bars are the sample sizes. The age of expanding leaves are the number of days (negative) before reaching full size (day 0), and the age of mature leaves is the number of days (positive) after full expansion.

## Methods

### Study site

The study was conducted between 1 March and 15 June, 1987 in a lowland moist forest on Barro Colorado Island (BCI), Panamá. Plants were sampled mainly in the young forest (approximately 70–100 yr old) (Foster and Brokaw 1982) along Shannon, Snyder-Molino, Lutz, and Barbour trails. Detailed descriptions of the BCI flora and recent studies conducted on the island can be found in Croat (1978) and Leigh et al. (1982).

### Host plant

*Gustavia superba* is an understory tree that ranges from Costa Rica to Colombia and is common as an adult in young forest on BCI. Seed predation and seedling survivorship have been studied by Sork (1985, 1987). Leaf production within the population is bimodal (Mori and Kallunki 1976). A highly synchronous flush of new leaves occurs after the first rains of the wet season, and another less synchronous flush occurs during the transi-

tion from the wet season to the dry season. Saplings of *G. superba* have a monopodal growth form and very large leaves (30–120 cm<sup>2</sup>). An individual will produce 3–12 new leaves in a single synchronous flush. Nectaries on the stipules surrounding the expanding leaves and food bodies on the veins of the young leaves attract ants that could defend the leaves against herbivores. However, we have never observed ants removing eggs of *E. priassus* and data from an ants exclusion experiment showed no difference in levels of herbivory to young leaves between controls and plants with ants excluded (T. M. Aide, unpubl. data).

### Major insect herbivore

*Entheus priassus* is a common insect herbivore on the young leaves of *G. superba*. Eggs are laid on the bud or on the expanding leaves and hatch 2–5 d later. When the first instar larvae emerge they cut part of the leaf at the margin, fold the leaf over and secure it with a silk thread. It takes approximately 49 d from the time of hatching to adult emergence with larvae passing through five instars [1<sup>st</sup> = 3.1 d, 2<sup>nd</sup> = 2.9, 3<sup>rd</sup> = 4.1, 4<sup>th</sup> = 8.8, 5<sup>th</sup> = 15.3, pupa = 15.0 (sample size for each stage  $\geq$  10)]. Pupation occurs off the host plant. On BCI, *E. priassus* has only been observed feeding on *G. superba*. The geographic range of *E. priassus* is not known, but it has been reported feeding on *G. ruiziana* and *Lecythis* sp. (Lecythidaceae) in Amazonia, Brazil (Moss 1949).

### Sampling procedure

One hundred saplings of *G. superba* (height 30–100 cm) were monitored daily for bud expansion. During the study 45 plants produced new leaves and of these 46% (21 plants) had one or more *E. priassus* egg laid on the young leaves. The leaf development and leaf quality of plants (at least three leaves per plant) with *E. priassus* were followed daily by measuring the leaf area, with a plastic grid, and the leaf toughness, with a Chatillon “penetrometer” (rod diameter = 3.2 mm). Although, the measurements made by the penetrometer may have affected the leaf chemistry, larvae that survived, fed on leaves that where measured in the same way as the leaves on which larvae did not survive. Leaves used for water content analysis were weighed immediately after collecting, dried at 40°C for 48 h, and then reweighed. Development of individual larvae was monitored daily.

Throughout the paper leaf characteristics and larval development are analyzed in relation to leaf age. Because the leaf area was measured daily, we know the day a leaf completed expansion. We define “day 0” as the day a leaf reaches full size. Thus, the age of an expanding leaf is the number of days (negative) before

Tab. 1. Survivorship data for *Entheus priassus* (67 eggs on 21 plants).

	Developmental stages					
	Egg	1st	2nd	3rd	4th	5th
# of larvae	67	56	38	29	25	20
% survivorship from one stage to the next		83.6	67.9	76.3	86.2	80.0

reaching full size, and the age of a mature leaf is the number of days (positive) after full expansion.

## Results

### Host plant characteristics

Bud swelling and leaf expansion was very rapid in *G. superba* (Fig. 1a). Between two and four days after the dormant bud began to swell, the expanding leaves were approximately 20% full size and could be measured without damaging the leaf. Leaves reached full size (day 0) four days later. Thus, *G. superba* produced a fully expanded leaf (30–120 cm<sup>2</sup>) from a small bud in six to eight days.

Increases in leaf toughness lagged behind leaf expansion (Fig. 1b). Leaf toughness increased only slightly up until day -1. There was a large increase between the day before full expansion (-1) and the day after (1) when toughness increased from approximately 0.11 MPa to 0.23 MPa. Over the remaining ten days, leaf toughness slowly increased to the level of a mature leaf (0.34 MPa).

The time course for water content in young leaves was negatively correlated with leaf toughness (Fig. 1c). The water content of approximately 1/4 expanded leaves was 85%. There was little change during expansion, but once the leaf was fully expanded and it began to toughen up, the water content declines. Ten days after the leaf was fully expanded the water content had dropped to 76%.

### Larval growth and survivorship

During the study, we found 67 eggs on 21 plants of which 83.6% developed to first-instar larvae (Tab. 1). Survivorship was lowest during the first and second instars. Although, some larvae disappeared between censuses, presumably due to predation, all first and second instar larvae were found dead on the leaf. These deaths were probably due to the inability of the early instars to feed on maturing leaves. Parasitoids are unlikely to have contributed to early-instar mortality because they have never emerged from dead or live larvae collected in the field and reared in the laboratory.

Fig. 2 shows the number of eggs that hatched on different aged leaves and the fate of the larvae. Larvae which hatched on expanding leaves (age < 0) had a

higher probability of surviving to third instar than did larvae which hatched on mature leaves (age ≥ 0) (Pearson Chi-square = 11.25, df = 1,  $p < 0.001$ ). Sixty-six percent of the eggs hatched on day -1 and day 0. Fourteen eggs hatched on day -1 and 10 survived (71.4%), but of the 17 eggs that hatched on day 0, only 3 survived (17.6%).

## Discussion

### Rapid leaf expansion: benefits

Previous work on herbivore food-plant choice has emphasized the difference between young and old leaves (Feeny 1970). Changes in leaf characteristics that decrease leaf palatability occur most dramatically soon

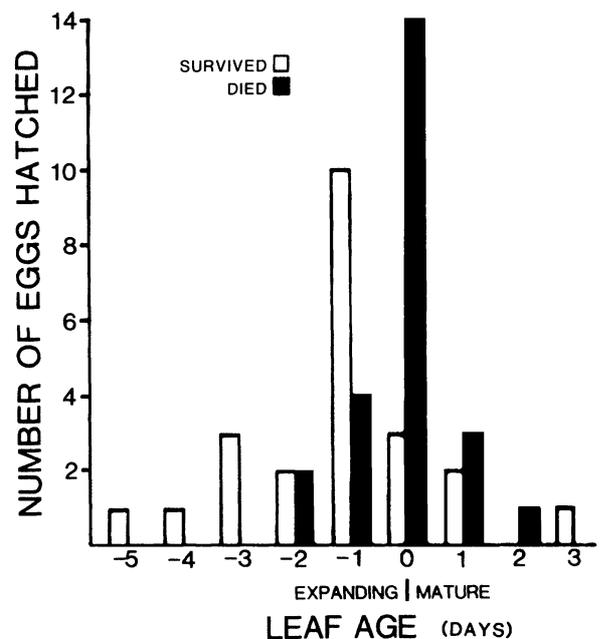


Fig. 2. Number of *E. priassus* larvae that survived and did not survive to third instar in relationship to the leaf age at time of hatching. The age of expanding leaves are the number of days (negative) before reaching full size (day 0), and the age of mature leaves is the number of days (positive) after full expansion.

Tab. 2. A comparison of leaf expansion rates and Kjeldahl leaf nitrogen content ( $\text{mg g}^{-1}$  in 1/10 fully expanded leaves) between *G. superba* and 13 common, shade-tolerant tropical trees (*Annona acuminata*, *Cnestidium rufescens*, *Connarus panamensis*, *Cupania sylvatica*, *Eugenia oerstediana*, *Guarea* sp. (hairy), *Licania platypus*, *Oouratea lucens*, *Rourea glabra*, *Talisia princeps*, *Tetragastris panamensis*, *Trichilia tuberculata*, *Xylopia macrantha*). Leaf expansion rates were calculated by determining the time, in days, for a leaf to double its area. Leaves were measured during the period of peak leaf expansion (10% to 70% full size). Data from T. A. Kursar and P. D. Coley (unpubl.).

	Leaf area doubling time (d)	Kjeldahl leaf nitrogen ( $\text{mg g}^{-1}$ )
<i>G. superba</i>	0.92	71.6
Mean $\pm$ SD of 13 species	1.99 $\pm$ 1.27	37.1 $\pm$ 11.3

after the leaf reaches full size (Feeny 1970, Mattson 1980, Scriber and Slansky 1981). Consequently, a rapidly expanding leaf that matures quickly and can rapidly employ the defenses of leaf toughness and decreased nutrient content, should receive less damage than a slowly expanding leaf. Species with rapid leaf expansion should benefit by reducing the time they are available for discovery by ovipositing females. Larvae feeding on these leaves will face a food substrate whose quality deteriorates at a faster rate, and, as a consequence, they may suffer greater mortality.

*G. superba* has an unusually fast leaf expansion rate. A leaf can expand from a small bud to a fully expanded leaf of  $100 \text{ cm}^2$  in about seven days. The leaf area doubling time of *G. superba* was twice as fast as the average of 13 common woody tree species on BCI (Tab. 2).

Other studies (Feeny 1970) have shown that seasonal changes in leaf characteristics can affect food plant choice and larval development, but for *E. priassus* feeding on *G. superba*, a time scale of only a few days is critical for larval survivorship. Larvae which hatch the day before the leaf is fully expanded are four times more likely to survive than larvae that hatch on the day the leaf reaches full size. The most obvious change in a leaf characteristics between day  $-1$  and day  $0$  is the increase in leaf toughness from  $0.11 \text{ MPa}$  to  $0.16 \text{ MPa}$ . If an ovipositing female does not encounter developing leaves by day  $-3$  the larvae are unlikely to survive because they hatch on leaves that are rapidly maturing. Larvae that hatch before the leaf is fully expanded are big enough by the time the leaves toughen that they can continue feeding and complete their larval cycle. These larvae will continue to eat the majority of the new leaves flushed by the plant. For *G. superba*, rapid leaf expansion may therefore function as a defense against young leaf herbivores. In addition, rapid leaf expansion should have major implications for herbivore search behavior, oviposition decisions, and egg development.

### Rapid leaf expansion: costs

A possible cost of rapid leaf expansion may be the high levels of nitrogen that are positively correlated with leaf expansion rates (T. A. Kursar and P. D. Coley, unpubl.). The Kjeldahl leaf nitrogen content of approximately 1/10 fully expanded leaves in *G. superba* was almost two times greater than the mean of 13 other woody species (Tab. 2). Nitrogen rich leaves are preferred food for herbivores (Mattson 1980). Although, rapid leaf expansion reduces the time young leaves are available to herbivores, if discovered, the high nitrogen content of the leaves make them a rich resource for herbivores. Generalist herbivores such as, brocket deer (*Mazama americana*) (T. M. Aide, pers. obs.) and sloths (*Bradypus variegatus*) (Montgomery and Sunquist 1978) occasionally eat all the young leaves on saplings and adults, respectively. Damage by insect herbivores other than *E. priassus* was mainly limited to expanding leaves and was highly variable suggesting that most young leaves escape damage, but when discovered they are devoured (T. M. Aide, unpubl. data). These observations support the idea that, if discovered by generalist herbivores, the nitrogen rich leaves will be consumed.

High levels of nitrogen may also accelerate larval development, increase larval survivorship, and result in greater leaf damage. In comparison with other Hesperidae, *E. priassus* appears to be a "fast" developing caterpillar (A. Aiello, unpubl. data). Although, rapid leaf expansion may have selected for the rapid larval development, an alternative explanation is a that rapid development is a facultative response to high leaf nitrogen.

### Conclusions

Although, a high proportion of a leaf's lifetime damage occurs during leaf expansion (Coley and Aide 1989), most studies have investigated plant defenses of mature leaves. When defenses of young leaves have been studied, neither physical nor chemical defenses have explained the variation in herbivory among species (Coley 1983). This study suggests that leaf expansion rate may act as an important herbivore defense for young leaves by reducing the time of this vulnerable stage. However, a constraint on the evolution of rapid leaf expansion will be the cost of losing leaves with high nitrogen content to opportunistic herbivores.

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## References

- Aide, T. M. 1988. Herbivory as a selective agent on the timing of leaf production in a tropical understory community. – *Nature*, Lond. 336: 574–575.
- Brattsten, L. B. 1979. Biochemical defense mechanisms in herbivores against plant allelochemicals. – In: Rosenthal, G. A. and Janzen, D. H. (eds), *Herbivores: their interaction with secondary plant metabolites*. Academic Press, New York, pp. 199–270.
- Brower, L. P. 1969. Ecological chemistry. – *Sci. Am.* 220: 22–29.
- Coley, P. D. 1983. Herbivory and defensive characteristics of tree species in a lowland tropical forest. – *Ecol. Monogr.* 53: 209–233.
- and Aide, T. M. 1989. A comparison of herbivory and plant defenses in temperate and tropical broadleaved forests. – In: Price, P. W., Lewinsohn, T. M., Benson, W. W. and Fernandes, G. W. (eds), *Herbivory: tropical and temperate perspectives*.
- Crawley, M. J. 1983. *Herbivory: the dynamics of animal-plant interactions*. – Univ. of California Press, Berkeley, CA.
- Croat, T. B. 1978. *Flora of Barro Colorado Island*. – Stanford Univ. Press, Stanford, CA.
- Feeny, P. 1970. Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillar. – *Ecology* 51: 565–581.
- Foster, R. B. and Brokaw, N. V. L. 1982. Structure and history of the vegetation of Barro Colorado Island. – In: Leigh, E. G., Rand, A. S. and Windsor, D. M. (eds), *The ecology of a tropical forest: seasonal rhythms and long-term changes*. Smithsonian Inst. Press, Washington, DC, pp. 67–81.
- Harborne, J. B. 1977. *Introduction to ecological biochemistry*. – Academic Press, London.
- Leigh, E. G., Rand, A. S. and Windsor, D. M. 1982. *The ecology of a tropical forest: seasonal rhythms and long-term changes*. – Smithsonian Inst. Press, Washington, DC.
- Lieberman, D. and Lieberman, M. 1984. The causes and consequences of synchronous flushing in a dry tropical forest. – *Biotropica* 16: 193–201.
- Mattson, W. J. 1980. Herbivory in relation to plant nitrogen content. – *Ann. Rev. Ecol. Syst.* 11: 119–161.
- McKey, D. 1979. The distribution of secondary compounds within plants. – In: Rosenthal, G. A. and Janzen, D. H. (eds), *Herbivores: their interaction with secondary plant metabolites*. Academic Press, New York, NY, pp. 55–133.
- (in press). Interactions between ants and leguminous plants. – In: Zarucchi, J. and Stirton, C. (eds), *Advances in legume biology*. Missouri Bot. Garden, St. Louis, MO.
- Milton, K. 1979. Factors influencing leaf choice by howler monkeys: a test of some hypotheses of food selection by generalist herbivores. – *Am. Nat.* 114: 362–378.
- Montgomery, G. G. and Sunquist, M. E. 1978. Habitat selection and use by two-toed and three-toed sloths. – In: Montgomery, G. G. (ed.), *The ecology of arboreal folivores*. Smithsonian Inst. Press, Washington, DC, pp. 329–359.
- Mori, S. A. and Kallunki, J. A. 1976. Phenology and floral biology of *Gustavia superba* (Lecythidaceae) in Central Panamá. – *Biotropica* 8: 184–192.
- Moss, M. A. 1949. Biological notes on some Hesperidae of Para and the Amazon. – *Acta Zool. Lilloana* 7: 27–79.
- Rathcke, B. J. and Poole, R. W. 1975. Coevolutionary race continues: butterfly larval adaptation to plant trichomes. – *Science* 187: 175–176.
- Scriber, J. M. and Slansky, F. 1981. The nutritional ecology of immature insects. – *Ann. Rev. Ent.* 26: 183–211.
- Shapiro, A. M. 1981. The pierid red-egg syndrome. – *Am. Nat.* 117: 276–294.
- Sork, V. L. 1985. Germination response in a large-seeded neotropical tree species *Gustavia superba* (Lecythidaceae). – *Biotropica* 17: 130–136.
- 1987. Effects of predation and light on seedling establishment in *Gustavia superba*. – *Ecology* 68: 1341–1350.
- Zucker, W. V. 1983. Tannins: does structure determine function? An ecological perspective. – *Am. Nat.* 121: 335–365.