Synchronous leaf production and herbivory in juveniles of *Gustavia superba*

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Summary. Synchronous leaf production has been proposed as a mechanism to reduce herbivore damage to young leaves by satiating herbivores. To test this hypothesis, I measured leaf production, leaf survivorship, and herbivore damage on juveniles of *Gustavia superba* (H.B.K.) Berg (Lecythidaceae), in two sites in Central Panama. Leaves were produced throughout the year, but there were peaks in leaf production at the beginning of the wet season. Plants that produced leaves synchronously with conspecifics received significantly less damage than plants that produced leaves out of synchrony, and high levels of leaf damage were correlated with shorter leaf lifetimes. These data suggest that plant phenology can influence risks of herbivory.

Key words: Herbivory – Leaf phenology – Panama – Tropics – *Gustavia superba*

In tropical forests, annual rates of herbivory are $\approx 11\%$, and, for many species, the majority of damage occurs during the first month when leaves are developing (Coley and Aide 1991). Information on defense characteristics of young leaves is crucial for the understanding of plant/herbivore interactions, but most research has focused on defense characteristics of mature leaves. Although young leaves may be chemically defended, high levels of water and nitrogen and low leaf toughness result in greater herbivore pressure (Coley and Aide 1991). Effective defenses of mature leaves, such as leaf toughness or high fiber content, are not viable if a leaf is still in the expansion stage.

Leaf phenology can play an important role in plant/herbivore interactions (Gage and Strong 1981; Lieberman and Lieberman 1984; Louda 1984; Shepherd 1985; Collinge and Louda 1989). Because young leaves are an ephemeral stage, the timing of leaf production may be under selection to reduce herbivore impact. For example, synchronous leaf production may reduce damage by satiating herbivores (Feeny 1976; Leigh and Smythe 1978; Coley 1983; Crawley 1986; Aide 1988; McKey

1989). This study tests the hypothesis that leaves produced in synchrony with conspecifics receive less damage than leaves produced out of synchrony. This hypothesis was tested by measuring leaf production, leaf survivorship, and herbivore damage on juveniles of a subcanopy tree *Gustavia superba,* for two years and in two populations in central Panama.

Methods

Study species. Gustavia superba (H.B.K.) Berg (Lecythidaceae) is a subcanopy tree with a distribution ranging from Costa Rica to Colombia (Croat 1978). In Panama, *G. superba* is widely distributed, occuring in dry, moist, premontane moist, and premontane wet forests (Croat 1978). Peak flowering occurs during the dry season (March and April) (Mori and Kallunki 1976) and fruit production occurs during the wet season (June and July) (Sork 1987).

Juveniles are monopodal and have large leaves (30–120 cm²). New growth, a flush of 3 to 12 new leaves, is accompanied by a small increment in stem height (1–10 cm) (pers. obs.). Leaf development is very rapid; young leaves expand from 20% full size to full size in four days (Aide and Londoño 1989). Rapid leaf development and maturation directly reduce larval survivorship of a young-leaf insect herbivore, *Entheus priassus* (Hesperiidae), by decreasing the time young leaves are available for early instar development (Aide and Londoño 1989).

Study sites. The study was conducted on Gigante Peninsula (Gigante population) and Barro Colorado Island (BCI) (Barbour population). Both populations are located within the Barro Colorado Nature Monument in central Panama. During the 10 years previous to the study, the mean ($\pm$ sd) annual rainfall in BCI was 2566 mm ($\pm$ 745 mm) (Windsor 1990). The majority of rain comes during the eight month wet season ($\approx$ April 15–December 15), but an occasional storm occurs during the four month dry season ($\approx$ December 15–April 15). Annual rainfall for the two years of this study (1986: 2221 mm, 1987: 2953 mm) were within one standard deviation of the 10-year mean.

The vegetation of this area of Panama is semideciduous lowland forest (Foster and Brokaw 1982). The forest on Gigante Peninsula is $\approx$ 45 years old (R. Foster, pers. com.), and most of the peninsula within 1 km of Gatun Lake, was under banana cultivation until the end of World War II (O. Kidd, pers. com.). Forests on steep slopes and areas away from the lake were the major seed sources for the regeneration of the cultivated land. Study plants were censused along the north end of the Ridge Trail, near "site a" of Sork (1987),

who studied seedling establishment of *G. superba*. Densities of *G. superba* seedlings were high ($\approx 40/100$ m²) on Gigante (Sork 1987). The forest on BCI is divided into the old forest, which has received little anthropogenic disturbance in the last 200–400 years, and the young forest, which has been cut and farmed to different degrees and is ≈ 80–100 years (Foster and Brokaw 1982). Plants were censused in the young forest along Barbour, Hood, and Van Tyne Trails. Densities of *G. superba* seedlings in the young forest of BCI were lower ($\approx 10/100$ m²) than on Gigante (Sork 1987).

Phenology, herbivory, and leaf survivorship. In January 1986, I tagged 50 juveniles (15–60 cm in height, ≈ 5 m apart) in the shaded understory on Gigante and, in April 1986, I tagged 100 juveniles (15–85 cm in height, ≈ 20 m apart) in the shaded understory on BCI (Barbour population). For each plant, I measured the height, counted the mature leaves, and marked the petioles of leaves with lightweight colored telephone wire. Leaf production was measured monthly for the next two years. Each time a plant flushed a cohort of leaves, I counted the number of leaves produced and marked the leaves with colored telephone wire to facilitate future identification. One month later, I measured the leaf area and the area damaged. For each cohort of leaves, the total area damaged was divided by the total potential leaf area to determine the proportion damaged in the first month. Leaf area and area damaged were measured using a plastic grid. The total potential leaf area was estimated to 1 cm² and damage was estimated to 0.1 cm². Buds that had been initiated, but were missing at the next census were not included in the analyses because the cause of loss (eg. herbivore or physical damage, or drought stress) could not be determined. Plants that died during the study were excluded from the analyses. Months were assigned as "peaks" in leaf production if the number of individuals producing new leaves was greater than twice the number expected if leaf production was uniform throughout the year.

In July 1987, I counted all the leaves on each plant and determined the survivorship of each cohort of leaves produced between May and December 1986 (intercensus period ranged from 14 to 7 months).

Statistics. Herbivory was calculated as the total area damaged divided by the total potential leaf area of a single flush. These data were first analyzed with the assumption that all flushes were independent. The effects of site (Gigante, Barbour), year (1986, 1987), and phenological classes (peak months, non-peak months) on levels of herbivore damage were determined. Two separate Mann-Whitney U analsyses of the effects of site and year on herbivory were not significant and, thus, the data were combined to test the effect of phenological class on herbivory. Fourthy eight individuals produced leaf flushes in both peak and non-peak months and the damage on these flushes was compared using a Wilcoxon sign rank test. If an individual produced more than one leaf flush in a phenological class (peak, non-peak) the mean of the values was used.

The relationship between herbivory and leaf survivorship was determined by counting the new leaves produced between May and December 1986, measuring the damage after the first month, and counting the leaves still on the plant 7 to 14 months later. These data were analyzed by Spearman rank correlation.

Results

Leaf phenology

Although leaves were produced throughout the year, both populations exhibited distinct peaks at the beginning of the wet season (Fig. 1). In the Barbour population, a third peak followed a large rain during the 1987 dry season (Fig. 1). At Gigante, 44% (1986) and 34% (1987) of the flushes occurred in the peak months. In the Barbour population, 44% (1987) of the flushes took place
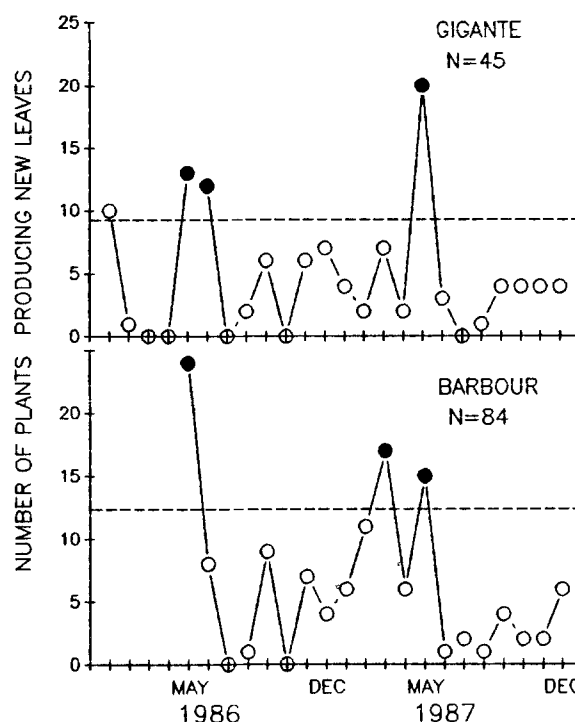

Fig. 1. The pattern of leaf production in the Gigante and Barbour populations during 1986 and 1987. Each data point represents the number of plants that had initiated leaf production since the previous census. The dashed line represents twice the expected value if leaf production were uniform throughout the year. Months with values greater than twice the expected value were classed as peaks (●) and all other months were classed as non-peaks (○). The first census of the Gigante population (January 1986) was not assigned as a peak month because approximately half these flushes should have been recorded for the previous month

during the peak months. Within a year, most plants produced leaves in a single phenological class (peak or non-peak) (Fig. 2). In comparison to Gigante, the Barbour population had a larger proportion of plants that did not produce any leaves and smaller proportion of plants that produced more than one flush (Fig. 2).

Herbivory

There was no significant effect of site (Mann-Whitney $U = 7836$, $p = 0.07$) or year (Mann-Whitney $U = 7734$, $p = 0.1$) on herbivore damage, but there was a significant effect of phenology class (Mann-Whitney $U = 3573$, $p < 0.001$) on damage (Fig. 3). In both sites and both years, damage was lower in the months of peak leaf production (6–13%) than in non-peak months (32–47%) (Fig. 3). For the 48 individuals that produced at least one cohort of leaves in both phenological classes, 37 had lower herbivore damage during the peak months (Wilcoxon Sign Rank Test; two-sided probability, $p < 0.001$).

Effect of herbivory on leaf survivorship

In both populations, leaf survivorship was significantly and negatively correlated with herbivory levels during the first month (Spearman rank correlation coefficient;
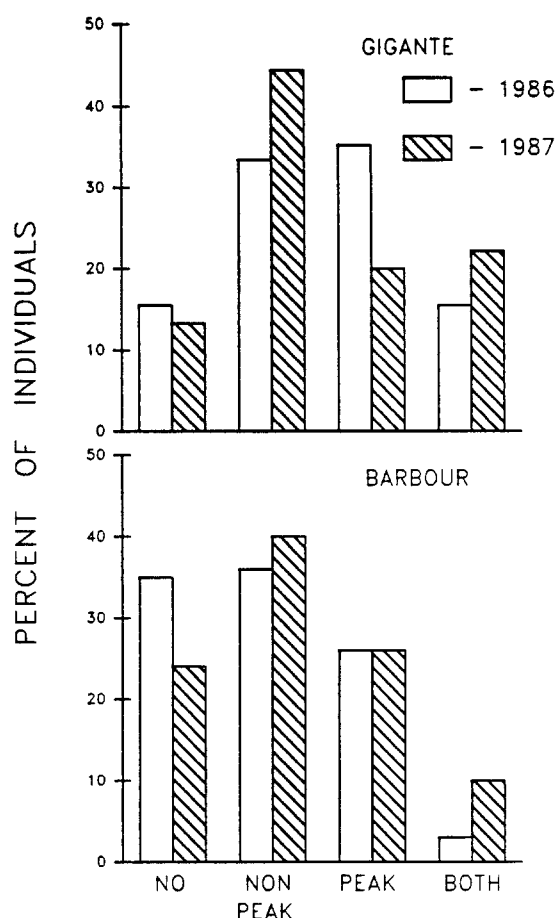
Fig. 2. The percentage of plants that did not produce any leaves (NO), produced leaves in one of the two phenological classes (NON–PEAK or PEAK), or produced leaves in both phenological class (BOTH) during a single year
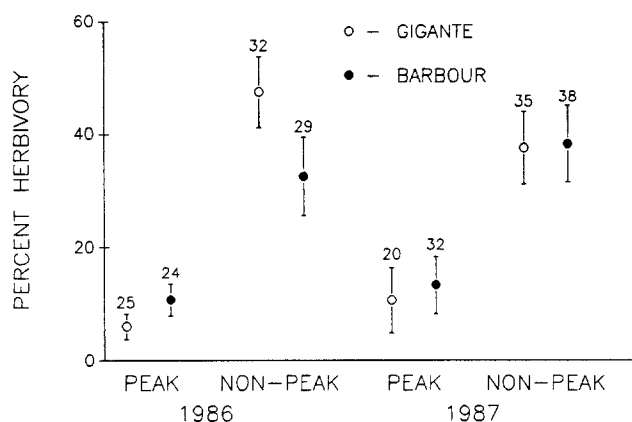

Fig. 3. The relationship between herbivory during the first month and the degree of synchronous leaf production or phenology class (peak and non-peak), during two years (1986 and 1987), and in two populations (Gigante and Barbour). The values reported are the mean ± SE and the number of flushes in each category

Gigante: $n=42$, $r=-0.618$, $p<0.01$, Barbour: $n=42$, $r=-0.334$, $p<0.05$). Leaf cohorts that received low levels of damage ($<20\%$) retained 84–88% of the leaves, while leaf cohort that received high levels of damage ($\geq 20\%$) retained between 30–60% of the leaves (Table 1).

Table 1. The relationship between young leaf herbivory and leaf survivorship. For each cohort of leaves produced between May and December 1986, I counted the number of leaves produced, measured the amount of damage after the first month, and counted the number of leaves still on the plant in July 1987. Plants were divided into two herbivory classes (low = damage < 20% and high = damage ≥ 20%). All leaf cohorts were not censused for the same length of time, therefore, I also report the mean ± SE intercensus period for each group

Population	Herbivory level	N	Percent leaf survivorship mean ± SE	Census Period (mo) mean ± SE
Gigante	low	27	87.9 ± 5.0	12.6 ± 0.4
	high	15	32.4 ± 10.9	9.0 ± 0.5
Barbour	low	28	84.3 ± 5.4	12.1 ± 0.5
	high	14	60.7 ± 11.6	10.1 ± 0.7

This relationship may be conservative because little damaged cohorts were mainly produced during the peak period at the beginning of the wet season and the time between censuses was longer (Table 1), thus, these plants had a longer period to lose leaves due to senescence or physical damage.

Discussion

The peak of *G. superba* leaf production occurs at the beginning of the wet season. At this time, plant water status improves and light levels may still be higher in mid-wet season, due to the deciduousness of some canopy individuals. Nevertheless, individuals of *G. superba* produced leaves throughout the year, implying that there may not be a severe physiological constraint on the timing of leaf production or that other factors may have influenced the pattern of leaf production.

For *G. superba*, leaves produced in synchrony with conspecifics received three to four times less herbivore damage than leaves produced out of synchrony. The same pattern was observed in two populations and in two years. Thus, this study supports that hypothesis that reduced young-leaf herbivory is associated with synchronous leaf production.

It is not clear whether the reduced damage is due to satiation of herbivores or to temporal escape from herbivores. By responding to the rains at the beginning of the wet season or to a large rain in the dry season, *G. superba* may be able to escape its herbivores by producing and maturing leaves before the herbivores can respond. For this species, the differences in the response time of the plant and the young-leaf herbivores are particularly important given the rapid leaf development of *G. superba* (Aide and Londoño 1989). Ovipositing females of *Entheus priassus*, a common herbivore of the young leaves, must encounter developing leaves at a very early stage because larval survivorship decreases dramatically if the larvae hatch on leaves that have completed development (Aide and Londoño 1989).

Regardless of the mechanism that causes syn-

chronously produced leaves to receive less damage, the high damage rates on leaves produced out of synchrony was correlated with shorter leaf survivorship. Shorter leaf survivorship would lead to lower lifetime carbon assimilation and a net loss of stored reserves. *Gustavia superba* juveniles often occur in the low light understory where carbon fixation is low and net growth is often zero (pers. obs.). If certain plants consistently receive high damage that reduced the photosynthetic area, leaf lifetime and stored reserves, then these plants would be less likely to resprout following damage caused by limb-falls, an important cause of mortality in the understory (Aide 1987; Clark and Clark 1989; Gartner 1989).

The relationship between synchronous leaf production and reduced herbivore damage is not restricted to tropical ecosystems. For example, phenologies of desert plants are severely constrained by abiotic factors and new leaf production is usually associated with peaks in rainfall. However, *Prosopis glandulosa* (honey mesquite) has deep roots with access to ground water and thus, has eliminated the dependence of growth on rainfall (Nilsen et al. 1987). Although *P. glandulosa* has continuous access to water, leaf production is highly synchronous and leaf development is very rapid. Nilsen et al. (1987) have argued that synchronous leaf production in *P. glandulosa* reduces damage rates to young leaves by reducing the time young leaves are vulnerable to herbivores.

This study and others suggest that the timing of leaf production can affect young-leaf herbivory. Leaf phenology will be most effective as a defense for species that produce leaves in synchronous flushes. Plants that produce leaves continuously are less likely to escape young-leaf herbivores and the defenses of these species will partially depend on their life history and light requirements (Coley 1983). Young leaves of continuously flushing shade tolerant species are often chemically well-defended (Macauley and Fox 1980). In tropical forest, most gap species produce leaves throughout the year and frequently defend young leaves by investing in extrafloral nectaries or ant attractants (McKey 1989). Schupp and Feener (1990) have shown that ant-defended species are more common in high light environments, and they argue that light (carbon) limitation in the understory selects againts extrafloral nectaries or ant attractants. Thus, if leaf phenology functions as a young-leaf defense, it would be most common in shade tolerant species with synchronous leaf production.

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