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## EFFECTS OF DEFOLIATION ON *ERYTHROXYLUM HAVANENSE*, A TROPICAL PROLEPTIC SPECIES<sup>1</sup>

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**Abstract.** Proleptic flowering is common among plant species from tropical seasonal forests. In these species flower initiation and anthesis are separated by a prolonged rest period (the unfavorable season), and the two processes are controlled separately. Proleptic species are appropriate for assessing the within- and between-season effects of herbivory on flowering and reproductive success. We investigated the reproductive consequences of artificial defoliation of the proleptic shrub *Erythroxylum havanense*, in a seasonal dry forest in western Mexico.

Twenty individuals in each of three sites were randomly assigned to one of four treatments: control (no manipulation), and three levels of leaf area removed: 0, 25, and 100%. Plants in the latter three treatments were sprayed with insecticide to prevent additional foliage consumption by natural herbivores.

Within a season undamaged plants (control and 0% defoliation) produced from two to four times more seeds than damaged ones (25 and 100% defoliation). In addition, completely defoliated plants exhibited a significant increase in both fruit maturation time (8 d) and average seed mass (9.5%), when compared to the plants in the other treatments. There was no evidence of a trade-off between seed number and seed mass, or between ripening time and seed mass.

One year after defoliation, vegetative growth (basal area increment) was reduced only by 100% defoliation. Likewise, flower and fruit production were significantly reduced only in this treatment. Although defoliation reduced seed production in both years, only the first year's reduction was a direct consequence of defoliation. Seed production decline in year 2 was an indirect effect of the reduction in flower number, suggesting that fruit and seed maturation do not depend on resources stored, but on annual production of photosynthates.

Plant survival was not affected up to 5 yr after defoliation.

Since most of the effects were evident only in the 100% defoliated plants, our results reflect those instances when insect outbreaks occur and *E. havanense* plants are completely defoliated.

**Key words:** artificial defoliation; between-season effects; *Erythroxylum havanense*; fitness components; proleptic species; seasonal tropical forest; western Mexico; within-season effects.

### INTRODUCTION

Herbivory is ubiquitous and has often been recognized as having a significant impact on plant fitness (Kulman 1971, Rockwood 1973, Waloff and Richards 1977, Bentley et al. 1980, Louda 1982a, b, Mills 1983, Horvitz and Schemske 1984, Kinsman and Platt 1984, Louda 1984, Marquis 1984, Clark and Clark 1985, Crawley 1985, Howe 1990, Milewski et al. 1991). Numerous studies of plants in both agricultural and natural settings have demonstrated the influence of herbivory on the reproductive success of plants and, in some instances, the evolutionary outcomes of herbivore-related plant attributes (Ehrlich and Raven 1964, Dirzo and Harper 1982, Berenbaum et al. 1986, Rausher and Simms 1989, Jaenike 1990, Marquis 1991,

Núñez-Farfán 1991, Zangerl et al. 1991). Some studies, however, have found no impact of moderate levels of herbivory (e.g., Núñez-Farfán and Dirzo 1991).

Although there is a considerable amount of work dealing with plant-herbivore interactions in temperate and tropical habitats (see Crawley 1983, and references therein), the effects of leaf tissue removal by herbivores have been poorly explored in tropical dry forests (see a review in Janzen 1981). Herbivory may be especially important in tropical dry forests, since their marked seasonality restricts plant growth (Opler et al. 1976, Reich and Borchert 1984). For most of the plant species in these habitats, the wet season is the only period when the resources for growth, reproduction, and maintenance, including survival through the dry season, are generated. Thus, in this system, leaf removal could have severe consequences.

Several plant species of tropical seasonal forests exhibit the phenomenon of proleptic flowering (Borchert

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1983). Proleptic species show discontinuous flower development, that is, flower initiation and anthesis are separated by a prolonged rest period (the unfavorable season), and both processes are controlled separately (Reich and Borchert 1984, Borchert 1992). Consequently, flower production and fruit maturation depend on two consecutive growing seasons. This fact could magnify the effects of herbivory, since reproductive success in a given season depends on the resources generated in that and the preceding season. No reports seem to be available on the effects of herbivory on proleptic species.

In this study we investigated the effects of experimental defoliation on *Erythroxylum havanense*, an abundant proleptic species in a seasonal dry forest in western Mexico. The specific question we addressed was: what are the consequences of moderate and complete defoliation on reproductive success and other components of fitness in both the same and the following season?

#### THE STUDY SYSTEM

This study was carried out in the Chamela Biological Station, located near the Pacific coast of Mexico (19°30' N, 105°03' W). Mean annual rainfall (1977–1987) is 699 mm, and 80% of the total precipitation falls between the months of July and October (Bullock and Solís-Magallanes 1990). The mean annual temperature is 24.9°C, and monthly averages range between 32.0° and 14.8°C. A detailed description of the climate of the Chamela region can be found in Bullock (1986). Elevation at this 1600-ha reserve ranges between 50 and 150 m. The predominant vegetation is tropical deciduous forest in the uplands and tropical semideciduous forest on arroyo sites. An account of the flora and vegetation structure of upland and arroyo forests of Chamela can be found in Lott et al. (1987).

*Erythroxylum havanense* (Erythroxylaceae) is a common understory deciduous shrub in the tropical dry forests of the Pacific coast of Mexico. In Chamela, flower anthesis and leaf production and expansion of this species are triggered by the first rains of the wet season (Domínguez 1990). Normally, the entire leaf production of a given season occurs in a single flush at the beginning of the rainy season. However, extensive damage by herbivores can cause additional leaf production (C. A. Domínguez, *personal observation*) and, presumably, increase costs to the plant. Typically, <5% of *E. havanense* leaf area is damaged by herbivores (Domínguez 1990). However, many plants at the Chamela population are severely defoliated (100%) when insect outbreaks occur (A. Pescador, *personal communication* and C. A. Domínguez, *personal observation*). Lepidopteran larvae (Saturniidae, Geometridae, and Lycaenidae) are the main herbivores of *E. havanense* at our study site. Several species of orthopterans are also found within the herbivore guild of this species, but they occur in small numbers.

#### METHODS

The effects of leaf area reduction on components of fitness of *E. havanense* were assessed by means of an artificial defoliation experiment. In July 1987 plants for this experiment were selected from three sites within the local *E. havanense* population. These sites were selected in order to cover the range of topographic variation in which this species occurs at Chamela. In each site we measured the size of all reproductive individuals of *E. havanense*. Because of the high occurrence of dead branches, size was measured as the sum of basal area of all living branches, and 60 study plants of comparable size (20 in each site) were selected. Within each site five plants were randomly assigned to one of the following treatments: control and one of three levels of artificial defoliation, 0, 25, and 100% of leaf area removed.

Defoliation treatments were applied in July 1987, 1 wk after flowering, when leaves were completely expanded. These treatments consisted of the removal of entire leaves. For the 25% treatment we counted all leaves on each individual and the fourth one out of each consecutive set of four was removed on a regular basis. Plants within defoliation treatments (0, 25, and 100%) were also sprayed with insecticide in order to prevent additional damage by natural herbivores. The insecticide we used belongs to the phosphoric acid group (Folimat, Bayer), which is characterized by high toxicity and low persistence (Ware 1978). The use of the treatments of 0% defoliation and 0% plus insecticide, allowed us to corroborate that the use of this insecticide did not have any undesirable effect on the plants. Insecticide was first applied 1 d after defoliation, and then weekly or after any rain that could wash it off from the leaves. This spraying continued until all marked plants had dropped their leaves at the end of the wet season (November 1987). All treatments were carried out 7 d after flowering, and thus we avoided any disturbance of natural pollination by experimental manipulation. Because the insecticide applications were done during the wet season, we did not consider it necessary to include a water control (no insecticide) within our experimental design.

The effects of this experimental defoliation on several fitness components were assessed during the years 1987 and 1988. For each marked plant, the number of flowers, initiated fruits (defined as the number of fruits present 5 d after flowering), and mature fruits were counted in 1987 and 1988. Fruit maturation time was measured as the time elapsed between fruit initiation (i.e., 5 d after flowering) and fruit ripening (defined by the intense red color of the fruits when they become mature). Immature green fruits suddenly become red-colored when they ripen, and thus fruit maturation can be readily defined. Since in this species mature fruits bear only one seed, fruit and seed number per plant are reliable and interchangeable estimations

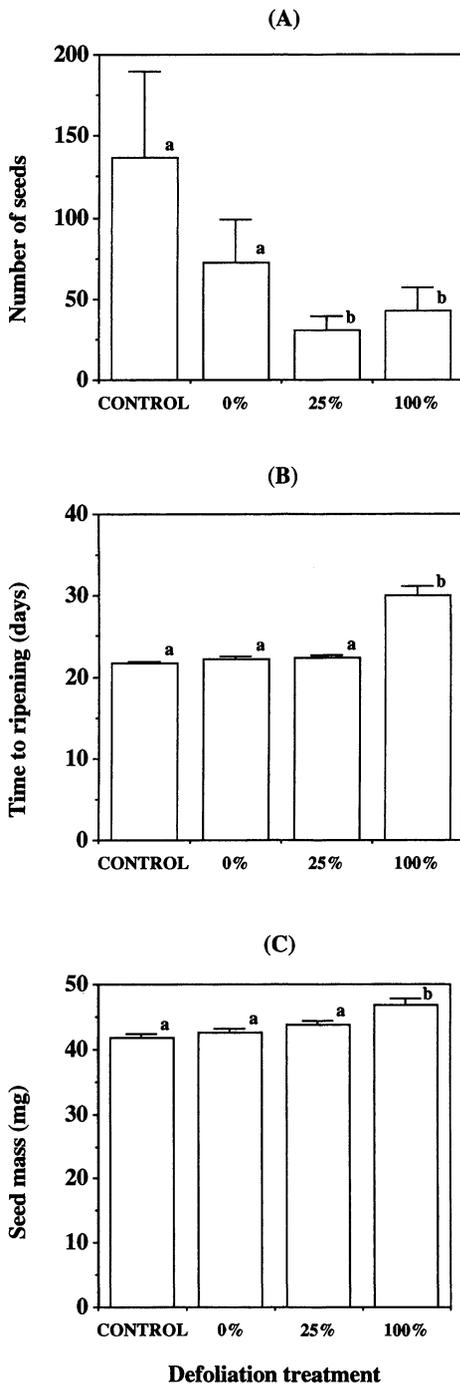


FIG. 1. Within-season effects of artificial defoliation of *Erythroxylum havanense* in Chamela, Jalisco, Mexico. Figures correspond to plant performance in 1987, the year of defoliation. (A) Number of seeds per plant. (B) Time to ripening (days to fruit ripening). (C) Seed mass per plant. Data are means and 1 SE. Treatments with the same letter indicate nonsignificant differences (ANOVA and a posteriori Tukey multisample comparisons;  $P > 0.05$ ).

of fitness. Seed wet mass (to the nearest 0.01 mg) was measured in both years with an analytical (Sartorius) balance. Individual plant growth was estimated as annual diameter increase (1987–1988), and this measure was also considered as a fitness component. Basal area measurements were performed  $\approx 3$  wk after the onset of the rainy season of both years.

Additionally, the effects of defoliation on plant survival were assessed during 1988 and 1992 by means of censuses of all marked plants. Plants were classified into two readily definable categories: healthy and dead or nearly dead plants (those with at least 90% of their branches dead).

Data analyses were mainly based on ANOVA. Most of the analyses included a covariate, because of this method's power to assign error variance to potentially confounding variables. In all reported results we verified that the assumptions of ANCOVA were met, i.e., that the covariates were homogeneous across treatments. Homogeneity of variances among treatments was evaluated by means of Bartlett's test. When necessary, data sets were transformed or nonparametric tests were applied. All results are presented as mean and 1 SE of untransformed data.

## RESULTS

### *Intersite differences*

There were no significant effects of site, nor site-treatment interactions on any of the analyzed variables ( $P = 0.091$ – $0.89$ ; see Domínguez 1990). Therefore, analyses were performed on the data pooled for all three sites. Analyses were carried out to assess the effects of defoliation on fitness components both within and between seasons.

### *Within-season effects (1987)*

Soon after being defoliated, plants within treatments of 25 and 100% of leaf area removed had a second flush of leaves. Reflushing was more pronounced in the completely defoliated plants. Plants in both 25 and 100% defoliation treatments had higher levels of fruit abortion in year 1 than those of undefoliated treatments. Average seed production among treatments was compared by means of ANOVA. We used a logarithmic transformation for seed number [ $\log(X + 1)$ ] to normalize the data (Zar 1974). Because of initial differences among plants in the number of initiated fruits, this variable was included as a covariate within the analysis.

Defoliation treatments had a significant effect on seed production in year 1 ( $F_{3,55} = 4.374$ ,  $P < 0.008$ ) (Fig. 1A). Defoliated plants (25 or 100%) produced fewer seeds (average of both treatments = 36.5 seeds) than undamaged plants (control and 0% plus insecticide, average = 104.5 seeds). In addition, a large proportion of the variance in seed production was accounted for by the covariate (number of initiated fruits) ( $F_{1,55} =$

128.766,  $P < 0.0001$ ), suggesting the dependence of seed production on phenomena occurring in the early stages of fruit development.

Experimental defoliation also had a significant effect on fruit maturation time in year 1 (Kruskal-Wallis'  $H = 31.061$ ,  $P < 0.0001$ ). Plants with 100% leaf area removed showed an 8-d delay in the time required for fruit maturation compared to plants in the other treatments (Fig. 1B). For the 100% defoliation plants, fruit development stopped after defoliation and did not resume until plants had produced a new flush of leaves.

Seed mass in year 1 was influenced by defoliation, but only in completely defoliated plants (Kruskal-Wallis'  $H = 26.6$ ,  $P < 0.0001$ ) (Fig. 1C). The average seed mass of completely defoliated plants was heavier (9.5%) than that of plants in the other treatments. This result could be a consequence of a trade-off between seed number and seed size. It could also be possible that seed mass and fruit maturation time are tightly linked in *E. havanense*, with heavier seeds resulting from longer fruit ripening times. In order to address these possibilities, we regressed seed mass on the number of seeds per plant and seed mass on fruit ripening time per plant. In both cases the data set consisted of more than one value of the  $Y$  variate for each value of the  $X$  variate; therefore, linear regression models with "replicates" were applied (see Sokal and Rohlf 1981). This method avoids the overestimation of the degrees of freedom brought about by the several measures of individual seed mass for each value of seed number or ripening time per plant.

Seed mass was independent of both the number of seeds per plant ( $F_{1,48} = 1.83$ ,  $P > 0.5$ ) and of ripening time ( $F_{1,13} = 0.753$ ,  $P > 0.5$ ). Thus, the heavier seed mass in 100% defoliated plants cannot be explained as a trade-off between seed mass and seed number, nor by the increased ripening times of plants within this treatment.

*Between-season effects (1988)*

Besides the short-term effects, artificial defoliation had statistically significant effects on several fitness components in the season following defoliation. The average basal area increment (1987–1988) was compared among defoliation treatments by means of ANOVA. There was a significant effect of defoliation ( $F_{3,56} = 3.39$ ,  $P = 0.024$ ) on plant growth. In this comparison, the 100% defoliation treatment was the only one that differed significantly from the others (Fig. 2A). The overall average basal area decrease of all plants ( $-0.24$  cm<sup>2</sup>,  $n = 60$ ) was in part a consequence of the high frequency of entire dead branches. Most plants had been attacked previously by xylophagous insects (microlepidoptera and coleoptera larvae) or were severely distressed by desiccation.

The number of flowers per plant 1 yr after defoliation differed significantly among treatments. An ANOVA, using the number of flowers per plant in 1987 as a

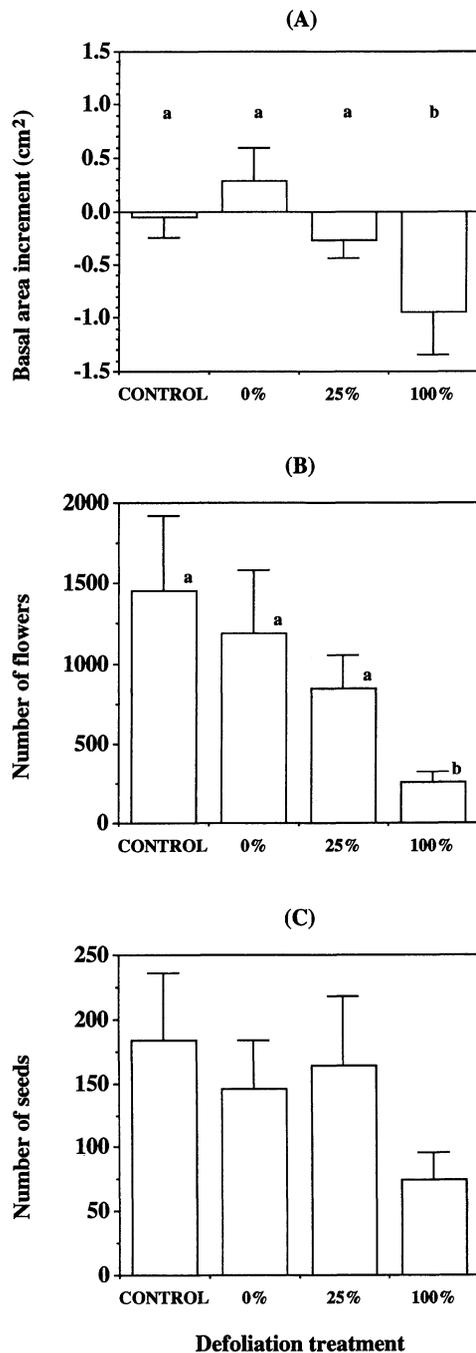


FIG. 2. Between-season effects of artificial defoliation in *Erythroxylum havanense* in Chamela, Jalisco, Mexico. Figures correspond to plant performance in 1988, 1 yr after defoliation. (A) Basal area increment per plant. (B) Number of flowers per plant. (C) Seed production per plant. Data are means and 1 SE. Treatments with the same letter indicate nonsignificant differences (ANOVA and a posteriori Tukey multisample comparisons;  $P > 0.05$ ).

covariate, showed that both the covariate ( $F_{1,55} = 17.86$ ,  $P < 0.0001$ ) and the treatments ( $F_{3,55} = 7.57$ ,  $P < 0.0001$ ) had a significant effect on flower production in 1988. Despite the tendency for a greater reduction in flower production at higher defoliation levels, it was significantly reduced only in the completely defoliated plants (Fig. 2B).

Additionally, completely defoliated plants showed a 54.8% reduction in their 1988 seed production compared to the other three treatments (Fig. 2C). In order to distinguish between the direct effects of defoliation on seed production and the indirect effects caused by the reduction in flower number, we carried out an ANOVA using the number of flowers as a covariate. Seed production was transformed as  $\log(\text{number of seeds per plant} + 1)$  (Zar 1974). While the effect of flower number on seed production was highly significant ( $F_{1,55} = 226.1$ ,  $P < 0.0001$ ), there was no effect of defoliation treatments ( $F_{3,55} = 1.78$ ,  $P = 0.16$ ), once the initial differences in flower number were accounted for by the covariate. An ANOVA using the percent of flowers setting fruits (fruit set; arcsine transformed) among treatments, gave similar results. Therefore, the observed reduction in seed production in 1988 was brought about as an indirect consequence of defoliation treatments via a decrease in flower number.

#### Effects on survival

Plant mortality 1 yr after defoliation was negligible (one plant). By 1992 the number of dead plants had increased to 25% (15 plants). However, plant mortality was independent of defoliation levels ( $\chi^2_3 = 0.98$ ,  $P > 0.9$ ).

#### DISCUSSION

With the exception of seed production in 1987, plants in the 25% defoliation treatment did not differ from undamaged plants (both control and 0% plus insecticide) in any of the measured variables. In contrast, high levels of defoliation (100%) had marked, negative consequences on *E. havanense*. Effects were evident on the 1987–1988 growth, ripening time in 1987, seed production and seed mass in 1987, and flower and seed production in 1988, but not on plant survival to 5 yr after defoliation.

The relative number of offspring contributed to the next generation by individual plants depends, among other things, on the number of flower buds, and the level of seed and fruit abortion. As our results showed, all of these phenomena are potentially affected by the activities of herbivores. Experimental defoliation brought about a marked reduction in fruit production in both years. However, only the 1987 reduction was a direct consequence of defoliation. The observed decline in seed production during 1988 was an indirect effect of the reduction in flower number. This result suggests that fruit and seed maturation do not depend on resources stored in plants, but on annual production

of photosynthates. Therefore, flower production (the potential number of fruits or seeds) and fruit maturation in *E. havanense* rely on temporally independent sources of energy. Accordingly, from the point of view of resource availability, successive reproductive seasons of *E. havanense* could be envisioned as independent events.

Since plants have no way to gauge forthcoming conditions, flower bud number in the current season cannot be adjusted to the next season's resource availability. Therefore, initiated fruits could need more energy than is available in the plant, generating an increase in the number of aborted fruits (Janzen 1976, Stephenson 1981, Sutherland 1986a, b). This could explain the relatively low fruit set we have observed in *E. havanense* under natural conditions ( $0.14 \pm 0.02$  [mean  $\pm 1$  SE],  $n = 120$ ; C. A. Domínguez, *personal observations*) when compared to a composite sample of 187 hermaphroditic species ( $0.22 \pm 0.14$ , Sutherland and Delph 1984, Sutherland 1986a). In any case, the relationship between the time of flower bud induction and the time of resource acquisition for fruit maturation could set a constraint on the evolutionary adjustment between flower number and resource availability. Thus, given this constraint and other things being equal, the overproduction of flowers is likely the best strategy under unpredictable conditions.

Defoliation caused a decrease in the number of flowers 1 yr after defoliation. It is likely that the production of a new leaf crop after complete defoliation exhausted a substantial amount of resources and diminished the allocation to bud production for the next reproductive season. This reduction has consequences on female and perhaps male components of fitness. Female fitness was clearly affected through the reduction of the potential number of seeds, while male fitness declined as a consequence of a decrease in pollen production and possibly pollinator attraction (see Charnov 1984, Lloyd 1987), although the latter was not measured. Additional experiments with *E. havanense*, in which fruit production and the abundance of pollinators in plants of variable flower number were monitored, showed a significant dependence of the number of flower visitors per plant on individual flower number (Domínguez 1990). In accordance, the reduced production of flowers in completely defoliated plants could cause an additional reduction in the number of pollinators visiting a plant and, consequently, in their potential as pollen donors.

Unexpectedly, seed mass was augmented in plants that were completely defoliated. Harper et al. (1970) have argued that seed mass is the least plastic reproductive component of yield, and numerous studies have documented reductions in the number of seeds but not seed mass as a consequence of herbivory (Maun and Cavers 1971, Rockwood 1973, Janzen 1976, Waloff and Richards 1977, Horvitz and Schemske 1984, Marquis 1984, Brown et al. 1987). However, recent studies

have shown seed mass not to be an entirely conservative character; moreover, some studies have also reported that seed size can be reduced by defoliation, whether artificial (Maun and Cavers 1971, Janzen 1976, Lee and Bazzaz 1980, Stephenson 1980, Brown et al. 1987) or by insects (Hartnett and Abrahamson 1979, Bentley et al. 1980, Kinsman and Platt 1984). However, this is one of the first studies that reports an increase in seed mass as a consequence of defoliation (see also Marshall et al. 1986). There is no simple interpretation for these results. Heavier seed mass in 100% defoliated plants of *E. havanense* was not explained as a trade-off between seed mass and seed number, nor by the increased fruit maturation time of plants within this treatment. A possible explanation may be that the plants cannot perfectly predict the availability of resources for seed filling. If completely defoliated plants underestimated the number of fruits they can fill, then it is possible that more resources were available for the remaining fruits. Since fruit abortion was higher in plants that were entirely defoliated, their leaf: fruit ratios were higher once a new flush of leaves was produced. This fact could augment the amount of available resources for seed filling and, consequently, seed mass.

Our study demonstrates that herbivory in *E. havanense* has the potential to reduce the reproductive output through two consecutive years. However, we do not know if this reduction is translated into a demographic effect (see Louda 1982a, b). Investigations with *Mirabilis hirsuta* (Kinsman and Platt 1984) and *Haplopappus squarrosus* (Louda 1982a, b) have shown that fruit dispersal and demography can be affected by herbivore-induced variations in the size of seed crops. Nonetheless, the present study indicates that independently of, or in addition to, a demographic effect, herbivores have a potential selective effect on the reproductive system of *E. havanense*.

Finally, the defoliation levels used in this study deserve consideration in the light of their potential realism. A census of the levels of natural herbivory in *E. havanense* at Chamela in 1987 and 1988, showed that levels of defoliation in the field were, on average, <5% of leaf area consumed (Domínguez 1990). Although such levels of damage may reflect the intensity of herbivory this species is regularly exposed to, our results can be readily extrapolated to natural conditions in such instances when insect outbreaks occur. Two such events have occurred between 1985 and 1992, and the affected plants were completely defoliated by geometrid caterpillars (C. A. Domínguez, *personal observation* and A. Pescador, *personal communication*). Thus our experiment mimics those circumstances that, although relatively infrequent, do occur in a plant's lifetime.

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