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Effects of defoliation on the saplings of a gap-colonizing neotropical tree

Núñez-Farfán, Juan & Dirzo, Rodolfo

Centro de Ecología, Universidad Nacional Autónoma de México, AP. 70-275, 04510 México D.F., Mexico; Tel. +52 5 5505485; Fax +52 5 5485259

Abstract. This paper describes a defoliation experiment on saplings of the gap-colonizing pioneer tree *Heliocarpus appendiculatus* in the tropical rain forest of Los Tuxtlas (Southeast Mexico). Four levels of defoliation (0, 25, 50, and 75% of the leaf area removed) were applied to naturally established plants in a medium-sized forest gap. Records were made of growth (height, diameter, and leaf production) and of whole-plant and leaf survival.

Statistical comparisons for all variables showed that plants that had not been defoliated grew better than defoliated ones, but there were no statistically significant differences between the defoliation levels. The risk of death was significantly lower for control plants than for defoliated plants at any level of damage. Leaf survivorship was highly irregular. The most consistent pattern was that the leaves of intact plants always showed higher survivorship, while the most heavily defoliated ones always had the poorest survival. The survivorship pattern of leaves at intermediate defoliation levels was irregular.

The results illustrate the lack of a monotonic response to a wide range of defoliation levels, and suggest the potential effect of herbivores as reducers of vegetative growth and survival in pioneer tropical species, and as limiting agents of plant establishment in regenerating forest gaps.

Keywords: Artificial defoliation; Growth; *Heliocarpus appendiculatus*; Herbivory; Los Tuxtlas; Pioneer tree; Sapling; Survival; Tropical rain forest.

Introduction

Herbivores may negatively affect one or more components of plant fitness (i.e. growth, survival, reproduction), and they have been considered as important selective agents in plant evolution (Ehrlich & Raven 1964; Feeny 1976; Rhoades & Cates 1976; Whitham & Mopper 1985; Marquis 1984). Over a limited period of time this selective process operates in terms of survival within a plant population, or reproductive differences, or both. Numerous studies have shown that defoliation, a common type of herbivory, acts negatively on plants (Harper 1977; Crawley 1983; Howe & Westley 1988), including reduction of growth rates (Morrow & LaMarche 1978), increased mortality (Kulman 1971 and references therein; Dirzo & Harper 1980), and decreased reproductive output (Jameson 1963; Waloff & Richards 1977; Rausher & Feeny 1980; Louda 1984; Marquis 1984; Crawley 1985; Whitham & Mopper 1985). The magnitude of the detrimental effect on an individual plant seems to be determined by the interaction of the amount of damage with other variables like, for example, type of tissue damaged, age or size of the plant, light, plant density, etc. (Lee & Bazzaz 1980; Dirzo 1984). Sometimes even a low level of herbivory may produce a measurable reduction in plant growth and fecundity (Louda 1984; Crawley 1985).

Studies in tropical forests have shown that herbivores may decrease adult plant fitness through a reduction of plant growth or reproductive output (Rockwood 1973; Marquis 1984; Mendoza, Piñero & Sarukhán 1987) and, may also to a lesser degree, reduce plant survival (see Mendoza, Piñero & Sarukhán 1987). Pioneer species that colonize, grow, and reproduce in treefall-gaps in these forests, frequently experience high levels of herbivory (Coley 1980, 1983; Dirzo 1987). Previous studies on *Heliocarpus appendiculatus*, a gap-colonizing species in the rain forest of Los Tuxtlas, have shown that herbivory in seedlings and saplings of this species can be high (up to 80%) and suggest that plant growth and survival may be affected by herbivore damage (Núñez-Farfán & Dirzo 1988). Reduction in growth has also been reported on seedlings of other tropical species (Lowman 1982; Becker 1983). Herbivory may also affect leaf longevity (Louda 1984; Pritchard & James 1984; Núñez-Farfán & Dirzo 1989) and leaf turnover-rate (Dirzo 1984; Louda 1984). However, it is not yet clear how effects on individual leaves may in turn affect the performance of a whole plant (see Hartnett & Bazzaz 1984; Núñez-Farfán & Dirzo 1989).

In this study we assessed the effects of artificial herbivory on the growth and survival of saplings of *Heliocarpus appendiculatus* Turcs. (*Tiliaceae*). In addition, we followed the fate of individual leaves under different leaf-area loss regimes.

Methods

The study was carried out at the Los Tuxtlas Tropical Research Station, a 700 ha preserve of lowland tropical rainforest, located in the state of Veracruz, southeastern Mexico (18°34'-18°36' N, 95°04'-95°09' W). Details of the vegetation and climate of the study site are given in Piñero, Sarukhán & González (1977).

In the rainy season of 1983 (end of August), a *Pseudolmedia oxyphyllaria* (*Moraceae*) tree, ca. 25 m tall, fell and opened a gap of ca. 200 m^2 in the forest canopy. A dense, pure stand of the pioneer species *Heliocarpus appendiculatus* became established there by early October 1983, and this population was used in this study.

H. appendiculatus is a large pioneer tree (up to 30 m in height), which grows fast and is short-lived (ca. 30 yr). It occurs only in forest gaps and disturbed areas in the forest, particularly clearings (Vázquez-Yanes 1980). The species produces many small, wind-dispersed fruits during the dry season (March-May), which are indehiscent, i.e. they do not open to release the seeds. The seeds may remain dormant in the soil for several months and have high germination rates if the ambient temperature fluctuates and reaches 31 °C or more, for a few hours a day (Vázquez-Yanes & Orozco-Segovia 1982); these conditions are normally met in gaps and clearings. Plants of this species usually bear evidence of intense defoliation throughout their life-cycle (Núñez-Farfán & Dirzo 1988). In a survey of the *H. appendiculatus* leaf-feeding insects, at least 10 species of *Lepidoptera* (several families) have been reared on this species' foliage (R. Dirzo unpubl.); most likely, the caterpillars of these species are responsible for most of the apparent damage.

Five 1 m^2 plots were randomly established over the gap area in which the saplings established. In late October 1983, all individual plants of *H. appendiculatus* in each plot were marked and, for each the height and basal diameter were measured. The point at which the diameter measurement was taken, was marked with permanent paint. A few days later (early November), undamaged individuals were randomly assigned to each of four experimental defoliation treatments on each plot: 0% (control), 25%, 50%, and 75% of the leaf area removed from each individual leaf present on the plant. Defoliation was done with scissors; care was taken to avoid damaging the main vein, in order to mimic, as far as possible, the normal defoliation situation for this species under natural conditions.

At intervals of about a month, we measured for all surviving individuals the diameter at the base of the stem (where the original measurement was made), total height, total number of leaves and number of new leaves produced (i.e. leaves produced between two successive recording dates). Surviving leaves and new ones on each individual were marked with colored plastic rings to distinguish cohorts of leaves. Hence, we were able to monitor, in addition to growth, both whole-plant and leaf survival through time (150 d). On each recording date, all new leaves were defoliated according to the plant's assigned treatment.

At the end of the experiment (March 1984), plants from each treatment were measured for total increment in diameter and height, and total number of leaves produced. A multivariate analysis of variance (MANOVA) was applied to assess the growth variables among plants undergoing different defoliation treatments.

Comparisons among survivorship curves of both whole plants and leaves under different defoliation regimes were performed using the Peto & Peto's Logrank Test (see Pyke & Thompson 1986).

Results

Growth

Two-way ANOVA tests did not reveal significant initial differences in the three growth parameters, neither among the plants assigned to each of the four defoliation groups ($P \geq 0.32$) nor among plots ($P \geq 0.06$) within the gap. The interaction plot × treatment was not significant either ($P \geq 0.19$). Thus, it was not necessary to use the plants' initial sizes as covariates for the subsequent analyses and, likewise, spatial heterogeneity did not lead to initial differences in growth parameters of the plants of the defoliation treatments.

Plant height (Fig. 1A) showed a similar response among all four defoliation groups up to day 100. After this, the control group diverged from and became significantly taller than the defoliated groups. A similar result was observed for mean basal diameter through time (Fig. 1B). By the end of the experiment the control plants showed on average a higher diameter than the defoliated plants. All groups of defoliated plants showed similar values for this parameter. The cumulative number of new leaves produced by plants subjected to the different defoliation treatments was highest on non-defoliated plants, while the means of all the defoliated plants were lower and similar (Fig. 1C).

A MANOVA showed significant effects of defoliation on the total gain in plant height and diameter, as well as on the total number of leaves produced per plant (Wilks' Lambda = 0.481, F = 4.639, DF = 12, 164, $P < 0.01$). Non-defoliated plants attained the higher values for all measurements of growth and differed significantly from the defoliated ones. The latter, in

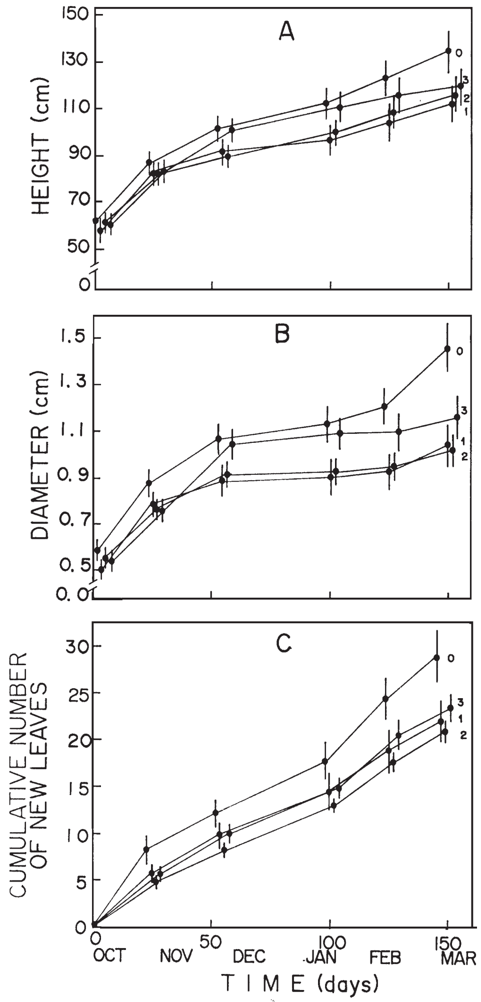

Fig. 1. Plant height (A), diameter (B) and new leaves produced (C), through time for saplings of *Heliocarpus appendiculatus* growing in a natural forest gap at Los Tuxtlas. The values are $\bar{x} \pm$ SE of four defoliation treatments: 0 = control group; 1 = 25%; 2 = 50%; and 3 = 75% of leaf area removed.

turn, constituted a statistically indistinguishable group (Table 1).

Survival of plants and leaves

Plant survival (Fig. 2A) was rather similar for all treatments at the beginning of the experiment (October). However, the survivorship curves diverged steadily and the final percentages of survival were 51, 36, 50, and 28% for the 0, 25, 50, and 75% defoliation groups, respectively. Survivorship of the 75% group was significantly lower than survivorship of the other three groups ($P < 0.05$). In other words, plant survival decreased significantly only as a consequence of the most

Table 1. Mean values (± SE) of total increment in height, diameter, and total number of new leaves produced per plant, for individual *Heliocarpus appendiculatus* undergoing different levels of defoliation. All increments correspond to a 150 days period. The values of *F* and *P* from the ANOVA are given for each variable. Means followed by the same superscript letter are not significantly different ($P > 0.05$, LSD Test). *N* = number of analyzed plants per group.

Defoliation Level	*N*	Total height increment(cm)	Total diameter increment (cm)	Total number of leaves
Control	25	47.2[a]	0.59[a]	29.64[a]
		(5.37)	(0.07)	(2.9)
25%	16	28.43[b]	0.24[b]	22.37[b]
		(4.32)	(0.04)	(1.97)
50%	20	30.7[b]	0.25[b]	20.7[b]
		(3.88)	(0.04)	(1.27)
75%	12	23.37[b]	0.18[b]	22.41[b]
		(3.41)	(0.03)	(1.83)
F	(DF = 3,69)	5.055	10.029	2.821
P		0.003	< 0.001	0.04

intense level of defoliation.

The survivorship curves of leaves (Fig. 2B) appear to be of the same shape for the different defoliation treatments within a given cohort. The first cohort of leaves (produced in October), for each defoliation level, showed a similar level of survival for the first month after defoliation. However, by the second month some differences were apparent. There were significant differences ($P < 0.05$) between the non-defoliated group and any group of defoliated leaves. Leaves of the second cohort differed significantly ($P < 0.05$) in survival according to the level of damage (Fig. 2B): survivorship of leaves of the 0 and 50% defoliation treatments was higher ($P < 0.05$) than that of the 25 and 75% groups. Finally, in the third cohort of leaves, significant differences ($P < 0.05$) were found between the groups 0, 25 and 50% defoliation versus the 75% group (Fig. 2B). Thus, for all cohorts the controls always showed the highest (or almost the highest) survivorship while the most heavily defoliated ones always had, significantly, the poorest survival.

Since non-defoliated plants produced more leaves during the period of study (Table 1), and the individual leaves on these plants showed a better survival on average, it would be expected that defoliated plants bore at the end of the study, a lower number of leaves. An ANOVA indicates that the standing number of leaves per plant of the defoliated groups was significantly lower than in the non-defoliated plants (*F* =

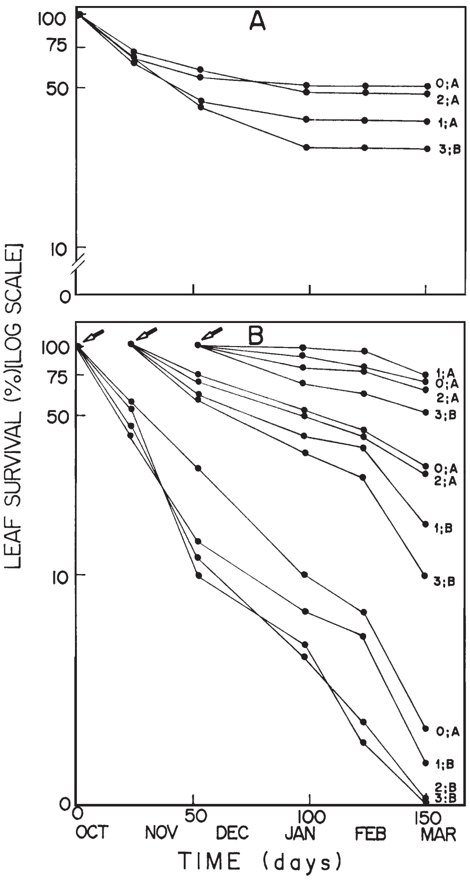

Fig. 2. (A) Survivorship curves for individual saplings of *Heliocarpus appendiculatus* undergoing different levels of defoliation. (Initial number of plants: 0 = 49; 1 = 44; 2 = 40; 3 = 43.) (B) Survivorship curves for three cohorts of leaves under different levels of defoliation. Arrows show the onset of the different cohorts. Initial number of leaves for the first cohort: 0 = 233; 1 = 127; 2 = 215; 3 = 154; second cohort: 0 = 114; 1 = 76; 2 = 77; 3 = 66; third cohort: 0 = 142; 1 = 77; 2 = 100; 3 = 76. Symbols as in Fig. 1. Different letters indicate statistically different groups according to the Peto & Peto Log-rank test (see text).

4.414, DF = 3, 69, $P < 0.01$), and there were no significant differences between the means of the defoliated plants. The means were 24, 18.7, 15.5, and 16 leaves per plant for the control, 25%, 50%, and 75% defoliation groups, respectively.

Discussion

A common caveat in artificial defoliation studies is that results may not reflect natural herbivory since this may be difficult to mimic. We recognize this problem and contend that applied levels of defoliation are at least within the natural range found in this species. Another constraint of this study is that only one gap was studied. Given that it is very difficult to have several comparable natural gaps (age, size, time of opening, patterns of colonization, etc.), and that internal heterogeneity of one gap can be as high as between gaps (see Núñez-Farfán & Dirzo 1988), our study represents only one of the various scenarios that could arise in tropical forests gaps. These constraints must be borne in mind in the following discussion.

The results of this study illustrate the growth potential of early colonizing individual plants of *H. appendiculatus*, and the extent to which it may be diminished by defoliation. For example, by the end of the study, when plants had reached an age of approximately 180 days, the control individuals attained an average height of 137 cm, and during the experimental period had increased their height by a factor of 2.2. These values contrast with the corresponding ones for the defoliated plants (all defoliation levels combined) of 114 and 1.9, respectively. Control plants grew significantly better than defoliated ones for all growth parameters measured, but the performance of the latter was similar and statistically indistinguishable - despite the wide range of applied defoliation levels. This result is striking, for it would be expected that increasing levels of defoliation would produce a corresponding increasingly negative effect on the growth parameters. Thus, it appears that *H. appendiculatus* is quite capable of withstanding high levels of defoliation. That the defoliated plants showed a similar growth performance suggests a capacity to compensate for some of the damage. Since we studied plants which were already well established (instead of newly-emerged seedlings), this may have offset the effects of defoliation. There is evidence that herbivory could be more important in its negative effect when the plant is younger (Harper 1977).

In contrast to the effects of defoliation on growth, the survival of whole-plants was significantly decreased only by 75% defoliation. Given that the plants of the intermediate defoliation levels showed diminished growth, it is possible that their risk of death will increase over a longer period of time. Since the studied population was damaged (due to reasons beyond our control) we were unable to monitor it for an extended period. Short-term effects on growth and longer-term effects on survival have been reported in other defoliation experiments with tropical plants (see Mendoza, Piñero & Sarukhán 1987).

We expected that the detailed analysis of the survivorship of populations of leaves would have helped us to understand the performance of whole plants (see Abul-Fatih & Bazzaz 1980; Bazzaz & Harper 1977). The most consistent pattern was that leaves of non-defoliated plants (in some cohorts they shared this status with leaves of intermediate defoliation levels). Furthermore, the leaves of the 75% defoliation level were always at the greatest risk of death and had, thus a dimished longevity. In contrast, the leaves of the 25 and 50% defoliation levels showed more erratic behavior - sometimes closer to the controls and sometimes closer to the 75% defoliation group. The demographic analysis of populations of leaves, coupled with the performance of individual plants, is an aspect that deserves more attention (e.g. leaf age-specific photosynthate contribution to the whole plant) (see Hartnett & Bazzaz 1984).

This study confirms previous suggestions (Núñez-Farfán & Dirzo 1988, 1989) that herbivory needs to be high to exert an appreciably negative effect on growth and survival in *H. appendiculatus*. This and the high levels of herbivory found in this species, support the contention that tropical pioneer species like *H. appendiculatus* probably do not allocate much of their resources to anti-herbivore defense (Coley 1988) and exhibit fast growth rates and rapid turnover of expendable leaves [e.g., the number of leaves produced by control plants was, on average, 29.6 (SE = 2.92, $N = 26$) per 150 days].

The results of this study also support the expectation that herbivores may constitute an important factor affecting individual growth and survival of tropical pioneer species (see Hartshorn 1975). Similarly, for light-demanding species like *H. appendiculatus* that depend on the attainment of height and exposure of leaf area for successful establishment in tree-fall gaps (cf. Ashton 1978; Bazzaz & Pickett 1980), the short-term effects of herbivory can be potentially serious on a longer-term basis.

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References

Abul-Fatih, H. & Bazzaz, F. A. 1980. The biology of *Ambrosia trifida* L. IV. Demography of plants and leaves. *New Phytol.* 84: 107-111.

Ashton, P. S. 1978. Crown characteristics of tropical trees. In: Tomlinson, P. B. & Zimmermann, M. H. (eds.) *Tropical trees as living systems*, pp. 591-615. Cambridge University Press, London.

Bazzaz, F. A. & Harper, J. L. 1977. Demographic analysis of the growth of *Linum usitatissimum*. *New Phytol.* 78: 193-208.

Bazzaz, F. A. & Pickett, S. T. A. 1980. Physiological ecology of tropical succession: a comparative review. *Ann. Rev. Ecol. Syst.* 11: 287-310.

Becker, P. 1983. Effects of insect herbivory and artificial defoliation on survival of *Shorea* seedlings. In: Sutton, S. L., Whitmore, T. C. & Chadwick, A. C. (eds.) *Tropical rain forest: ecology and management*, pp. 241-252. Blackwell, Oxford.

Coley, P. D. 1980. Effects of leaf age and plant life history patterns on herbivory. *Nature* 284: 545-546.

Coley, P. D. 1983. Herbivory and defensive characteristics of tree species in a lowland tropical forest. *Ecol. Monogr*. 53: 209-233.

Coley, P. D. 1988. Effects of plant growth rate and leaf-time on the amount and type of anti-herbivore defense. *Oecologia (Berl.)* 74: 531-536.

Crawley, M. J. 1983. *Herbivory: the dynamics of animal-plant interactions*. Blackwell, Oxford.

Crawley, M. J. 1985. Reduction of oak fecundity by low-density herbivore populations. *Nature* 314: 163-164.

Dirzo, R. 1984. Herbivory: a phytocentric overview. In: Dirzo, R. & Sarukhán, J. (eds.) *Perspectives on plant population ecology*, pp. 141-165. Sinauer Ass., Sunderland, Mass.

Dirzo, R. 1987. Estudios sobre interacciones planta-herbívoro en Los Tuxtlas, Veracruz. In: Clark, D. A., Dirzo, R. & Fetcher, N. (eds.) Ecología y ecofisiología de plantas en los bosques mesoamericanos. *Rev. Biol. Trop.* 35 (Suppl. 1): 119-131.

Dirzo, R. & Harper, J. L. 1980. Experimental studies on slug-plant interactions. II. The effect of grazing by slugs on high density monocultures of *Capsella bursa-pastoris* and *Poa annua*. *J. Ecol.* 68: 981-1011.

Ehrlich, P. R. & Raven, P. H. 1964. Butterflies and plants: a study in coevolution. *Evolution* 18: 586-608.

Feeny, P. P. 1976. Plant apparency and chemical defense. In: Wallace, J. M. & Mansell, M. (eds.) Biochemical interaction between plants and insects. *Rec. Adv. Phytochem.* 10: 1-40.

Harper, J. L. 1977. *Population biology of plants*. Academic Press, London.

Hartnett, D. C. & Bazzaz, F. A. 1984. Leaf demography and plant-insect interactions: goldenrods and phloem-feeding aphids. *Am. Nat.* 124: 137-142.

Hartshorn, G. S. 1978. Tree falls and tropical forest dynamics. In: Tomlinson, P. B. & Zimmermann, M. H. (eds.) *Tropical trees as living systems*, pp. 617-638. Cambridge University Press, London.

Howe, H. F. & Westley, L. C. 1988. *Ecological relationships of plants and animals*. Oxford University Press, New York.

Jameson, D. A. 1963. Responses of individual plants to harvesting. *Bot. Rev.* 29: 532-594.

Kulman, H. M. 1971. Effects of insect defoliation on growth and mortality. *Ann. Rev. Entomol.* 16: 289-324.

Lee, T. D. & Bazzaz, F. A. 1980. Effects of defoliation and competition on growth and reproduction in the annual plant *Abutilon theophrasti*. *J. Ecol.* 68: 813-821.

Louda, S. M. 1984. Herbivore effect on stature, fruiting, and leaf dynamics of a native crucifer. *Ecology* 65: 1379-1386.

Lowman, M. D. 1982. Effects of different rates and methods of leaf area removal on rain forest seedlings of coachwood

(*Ceratopetalum apetalum*). *Aust. J. Bot.* 30: 477-483.
Marquis, R. J. 1984. Leaf herbivores decrease fitness of a tropical plant. *Science* 226: 537-539.
Mendoza, A., Piñero, D. & Sarukhán, J. 1987. Effects of experimental defoliation on growth, reproduction and survival of *Astrocaryum mexicanum*. *J. Ecol.* 75: 545-554.
Morrow, P. A. & LaMarche, V. C. 1978. Tree ring evidence for chronic insect suppression of productivity in subalpine *Eucalyptus*. *Science* 201: 1244-1246.
Núñez-Farfán, J. & Dirzo, R. 1988. Within-gap spatial heterogeneity and seedling performance in a Mexican rain forest. *Oikos* 51: 274-284.
Núñez-Farfán, J. & Dirzo, R. 1989. Leaf survival in relation to herbivory in two tropical pioneer species. *Oikos* 54: 71-74.
Piñero, D., Sarukhán, J. & González, E. 1977. Estudios demográficos en plantas. *Astrocaryum mexicanum* Liebm. I. Estructura de las poblaciones. *Bol. Soc. Bot. Méx.* 37: 108-118.
Pritchard, I. M. & James, R. 1984. Leaf mines: their effect on leaf longevity. *Oecologia (Berl.)* 64: 132-139.
Pyke, D. A. & Thompson, J. N. 1986. Statistical analysis of survival and removal rate experiments. *Ecology* 67: 240-245.
Rausher, M. D. & Feeny, P. P. 1980. Herbivory, plant density, and plant reproductive success: the effect of *Battus philenor* on *Aristolochia reticulata*. *Ecology* 61: 905-917.
Rhoades, D. F. & Cates, R. G. 1976. Toward a general theory of plant antiherbivory chemistry. In: Wallace, J. M. & Mansell, R. J. (eds.) Biochemical interaction between plants and insects. *Rec. Adv. Phytochem.* 10: 168-213.
Rockwood, L. L. 1973. The effect of defoliation on seed production of six Costa Rican tree species. *Ecology* 54: 1363-1369.
Vásquez-Yanes, C. 1980. Notas sobre la autoecología de los árboles pioneros de rápido crecimiento de la selva tropical lluviosa. *Trop. Ecol.* 21: 103-112.
Vásquez-Yanes, C. & Orozco-Segovia, A. 1982. Seed germination of a tropical rain forest pioneer tree (*Heliocarpus donnell-smithii*) in response to diurnal fluctuation of temperature. *Physiol. Plant*. 56: 295-298.
Waloff, N. & Richards, O. W. 1977. The effect of insect fauna on growth, mortality and natality of broom, *Sarothamnus scoparius*. *J. Appl. Ecol.* 14: 787-789.
Whitham, T. G. & Mopper, S. 1985. Chronic herbivory: impacts on architecture and sex expression on pinyon pine. *Science* 228: 1089-1091.

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