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Author(s): Marlene de la Cruz and Rodolfo Dirzo

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# A Survey of the Standing Levels of Herbivory in Seedlings from a Mexican Rain Forest<sup>1</sup>

Marlene de la Cruz and Rodolfo Dirzo<sup>2</sup>

Departamento de Ecología, Instituto de Biología, UNAM, Apdo. Post. 70-233, México 04510

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## ABSTRACT

The standing levels of herbivory on the foliage of seedlings were measured for 52 species from Los Tuxtlas forest in southeastern Mexico. The level of damage averaged 10 percent or less; only a minimum of the sample showed extensive damage. Several types of damage to foliage were distinguished; some species displayed a predominance of one type, whereas other species sustained a variety of types. Besides pathogenic and physical damage, insects were the herbivores responsible for all of the damage. The interspecific variation in levels of herbivory could not be explained on the basis of plant life history or growth form. We suggest that plants with different life histories employ equally successful (or unsuccessful) antiherbivore mechanisms.

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## RESUMEN

Se midieron los niveles de herbivorismo presentes en el follaje de las plántulas de 52 especies de Los Tuxtlas (Sureste de México). Las mediciones se hicieron en un solo momento para cada especie. Se encontró que el nivel de daño promedio fue del orden de 10 por ciento o menos; solamente una mínima fracción de la muestra analizada presentó niveles de daño considerables. Se detectaron los tipos de daño presentes en el follaje; unas especies mostraron predominancia de un solo tipo, mientras que otras tuvieron varios de ellos. Además de los patógenos y el daño de tipo físico, los insectos fueron los agentes responsables de la mayoría del daño, pero ésta no pudo explicarse con base en la historia de vida de la planta o su forma de crecimiento. Se sugiere que plantas con diferente historia de vida emplean mecanismos anti herbívoro que son igualmente eficientes (o ineficientes).

LEVELS AND PATTERNS OF HERBIVORY in natural communities have been investigated for a few tropical localities (Odum & Ruiz-Reyes 1970, Leigh & Smythe 1978, Janzen 1981, Johnstone 1981, Coley 1980, Dirzo 1984), and most studies have concentrated on the analysis of the foliage of mature or juvenile trees. Janzen (1981) has investigated patterns and levels of damage on seeds, but in no cases have studies been made on the seedling community, despite the fact that seedling herbivory may have a profound impact on individual plants and thus be an important selective agent. Even if lethal to a seedling, damage may or may not play an important demographic role as a population-regulating agent (see Harper 1977, Louda 1982). The study of the interaction between herbivores and plants at the seedling level, with the aim of defining its importance as a selective and regulatory agent and its role in population recruitment and forest regeneration, has yet to be initiated for tropical systems. Presently, the number of unanswered questions, even at the very basic level of defining the intensity and patterns (if any) of herbivory, is still overwhelming.

Patterns and levels of herbivory on seedlings are expected to be different from those reported for mature or juvenile plants if only because the guilds of herbivores operating on the forest floor are likely to differ from those

of upper strata. In particular, a number of vertebrate folivores are abundant at ground level but not in the forest canopy, and vice versa; this is probably true for a number of invertebrates (see Janzen 1983).

As a first approximation to the long-term study of herbivory on seedlings in Los Tuxtlas rain forest, the foliage of seedlings from this forest was sampled to answer the following questions: What is the extent of herbivore damage to foliage in the seedling community? What herbivores are responsible for the removal of leaf tissue from the seedlings? Are any patterns detectable in the variation of the levels of damage in the community? Patterns of interest include some species' experiencing more damage than others and the presence of common characteristics for species with different degrees of herbivory. For this preliminary study the standing levels of herbivory (rather than their rates) on the leaves from a representative number of species at the Los Tuxtlas forest were sampled.

## STUDY SITE

The study was carried out at the Los Tuxtlas Research Station, a tropical rain forest preserve of 700 ha located in the southeastern part of the State of Veracruz, Mexico (95°07'W, 18°36'N). The vegetation of the station is classified as selva alta perennifolia (Miranda & Hernández-X. 1963)—a tall and diverse evergreen forest with trees to 30 m high. Characteristically, the lowest part of

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<sup>2</sup> Present address: Estación de Biología Los Tuxtlas, UNAM, Ap. Post 94, San Andrés Tuxtla, Ver., Mexico.

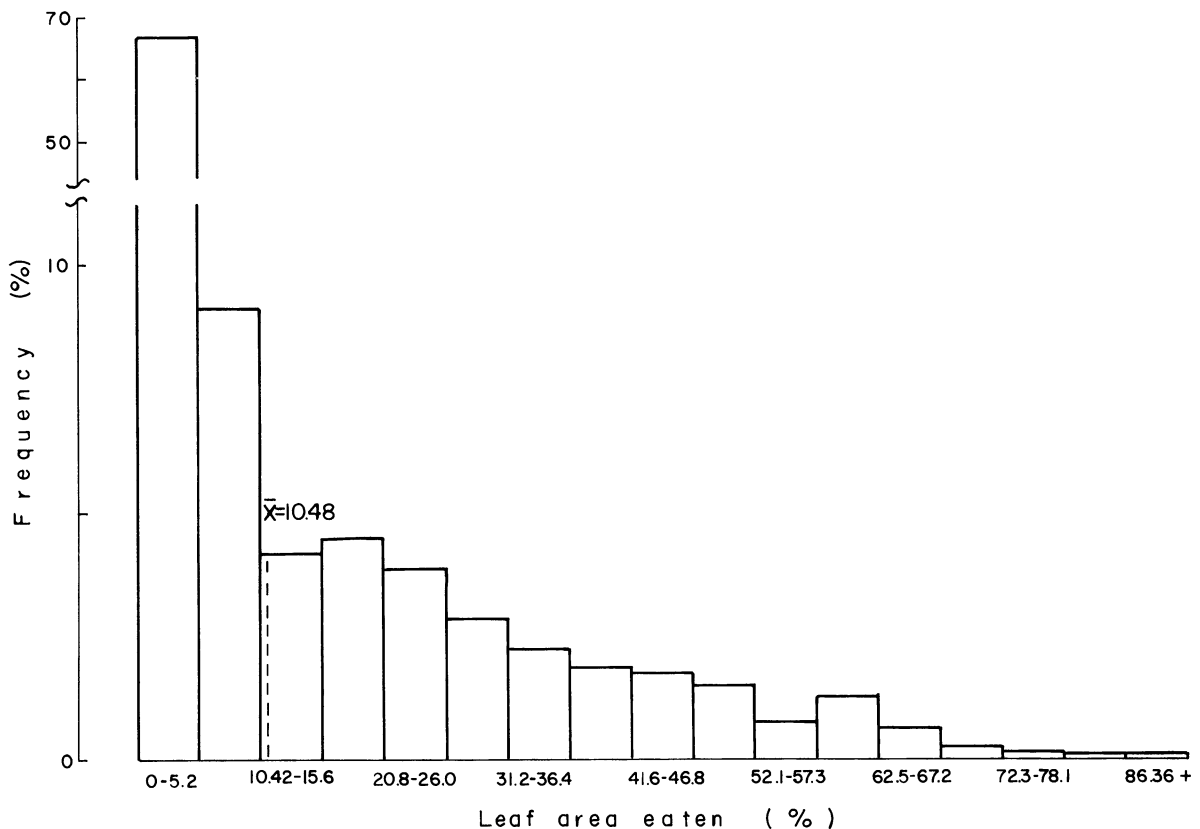


FIGURE 1. Frequency distribution of damage on a per-sample basis for 3394 leaves from 1697 seedlings sampled at Los Tuxtlas. Damage measured to the nearest mm<sup>2</sup>, using a leaf-area scanner. The broken line represents the mean (10.5%) for all sampled leaves.

the forest's understory is carpeted with the seedlings from a large number of trees and lianas, as well as several species of ferns and herbs. Annual rainfall in the forest averages 4725 mm, with a relative dry season (April–May) in which rainfall drops to 200 mm and a winter wet season (November–February) that accounts for up to 15 percent of total annual rainfall. Mean temperatures of the forest range from 17°C (January) to 29°C (June). More detailed accounts of the physical and biotic characteristics of the station can be found in Lot-Helgueras (1976).

## MATERIALS AND METHODS

From September 1983 to August 1984, 2 leaves/plant from seedlings of 52 species were collected from several areas of the forest so that the sample would include plants representative of different life histories (pioneers, nomads, and shade tolerants [Martínez-Ramos, 1985]), and growth forms (trees, lianas, and herbs). Seedlings were defined as those young individuals (up to 4 yr old for long-lived species and 6 mo old for herbs) bearing at least 4 leaves

(not cotyledons). Seedling height was not a criterion since it varies extremely among species. From each individual seedling the 2 lowest (oldest) leaves were collected to insure that, since leaf production is not markedly seasonal, the leaves have been exposed to attack by herbivores for most of their life span.

A sample of 50 leaves/species was randomly chosen from all the leaves collected for each taxa, after applying a running-variance analysis (see Greigh-Smith 1983) to determine sample size. For each leaf, the percentage of area lost to herbivores was calculated by measuring (to the nearest mm<sup>2</sup>) the total and the missing leaf areas with a leaf-area scanner (Li-Cor, Li 3100). The average of the 50 measurements, which is the mean percentage of leaf area eaten by herbivores, was then determined for each species. In all, 3394 leaves from 1697 seedlings were analyzed. For a subsample of 15 species, all the leaves ( $N = 2800$ ) were assigned to previously defined types of damage by herbivores (see Balick *et al.* 1978, Hendrix & Marquis 1983, Dirzo 1984) in order to define groups of herbivores responsible for the damage.

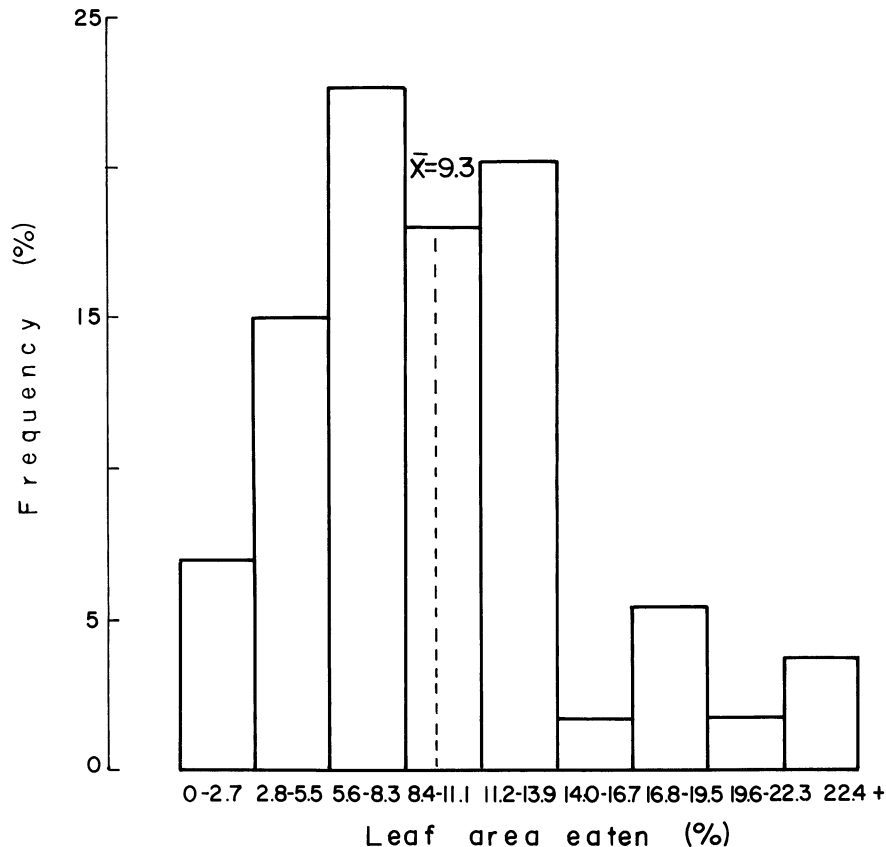


FIGURE 2. The frequency distribution of mean leaf area eaten (%) on a per-species basis for 52 species in the Los Tuxtlas forest. The broken line represents the mean (9.3%) for all species.

## RESULTS

The complete list of species analyzed, dates of collection, and a summary of results is shown in Table 2.

The first level of analysis (Fig. 1) shows the frequency distribution of damage to the 3394 leaves. The distribution of categories of leaf area eaten is extremely skewed: 76 percent had damage levels lower than the mean ( $\bar{x} = 10.5\%$ ), but 41 percent of the leaves were intact. Thus, only about 24 percent of the sampled leaves were more than 10 percent damaged. Moreover, a minimum of the sample (0.5%) shows damage greater than 25 percent.

When the data are averaged on a per-species basis (Fig. 2), some of the variation is concealed, the range is reduced, and the histogram becomes much less skewed. The mean leaf area eaten per species is now 9.3 percent. More than half of the sampled species (86.79%) show levels of damage below the grand mean. The upper averaged value of leaf area eaten per species is 24.2 percent, and only a few species (13.20% of the total) show levels of damage between 15 percent and the upper value. Thus, on either a per-species or a per-sample basis, modal levels

of herbivory on seedlings appear to be rather low at 10 percent or less.

Although the levels of herbivory appear to be somewhat restricted, some degree of interspecific variation occurs within the observed range. A plausible source of heterogeneity is that related to differential herbivory as a function of plant life history and successional status (Cates & Orians 1975; Coley 1980, 1983a; Hartshorn 1980). Forty-three of the 52 sampled species could clearly be classified as pioneers (15 species), nomads (15 species), or tolerants (13 species) (categories as defined by Martínez-Ramos [1984]). The mean percentage of leaf area eaten for each of these life history categories shows (Fig. 3a) an order of pioneers > nomads > tolerants. However, much variation occurs within each of the categories, and a Kruskal-Wallis multisample comparison (Zar 1974) using the untransformed values detected no significant differences between the three categories ( $0.10 > P > 0.05$ ). (The same result was obtained applying an ANOVA to the arc-sine transformed values.) When the species were grouped on the basis of their growth form (herbs, trees,

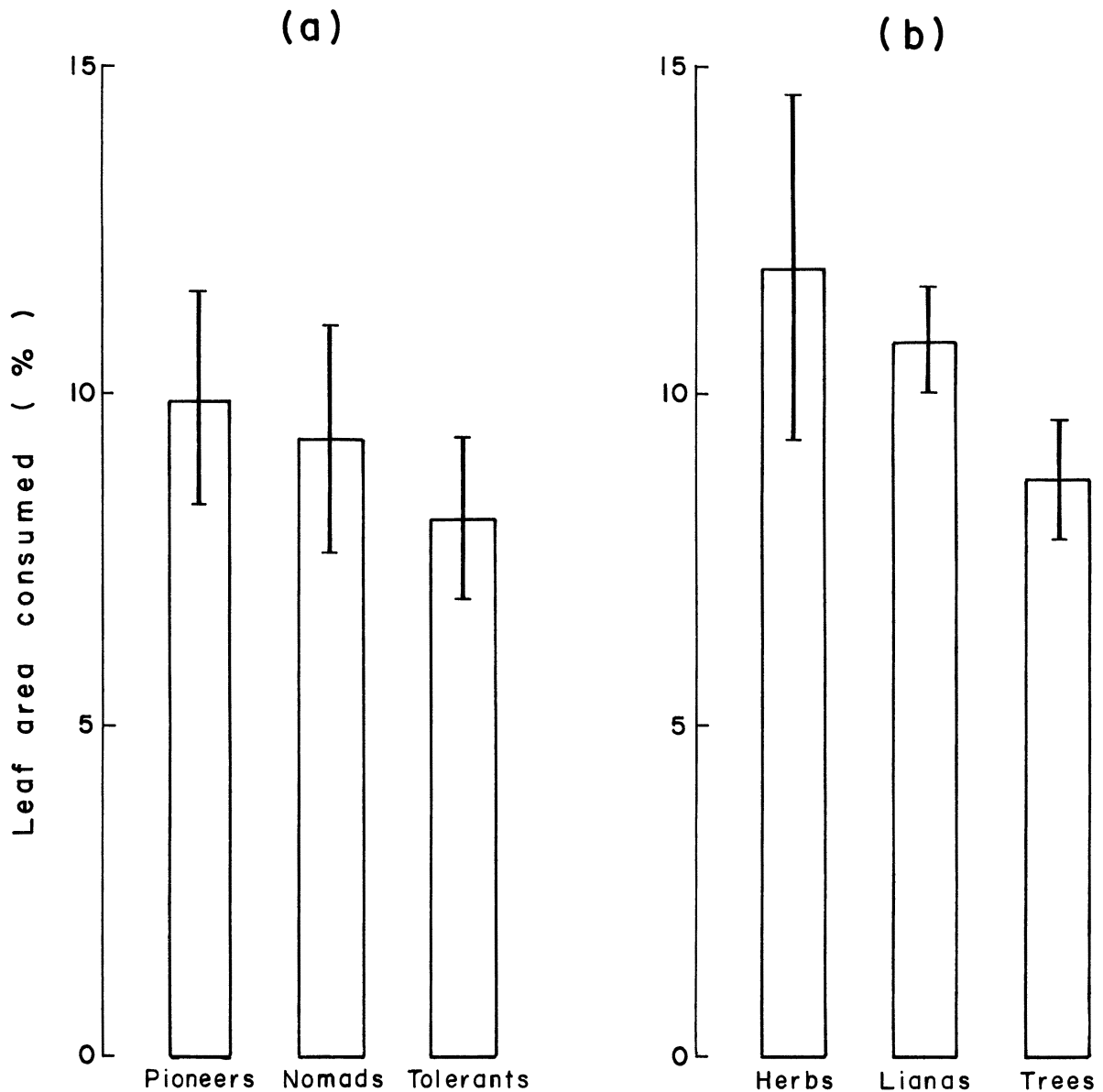
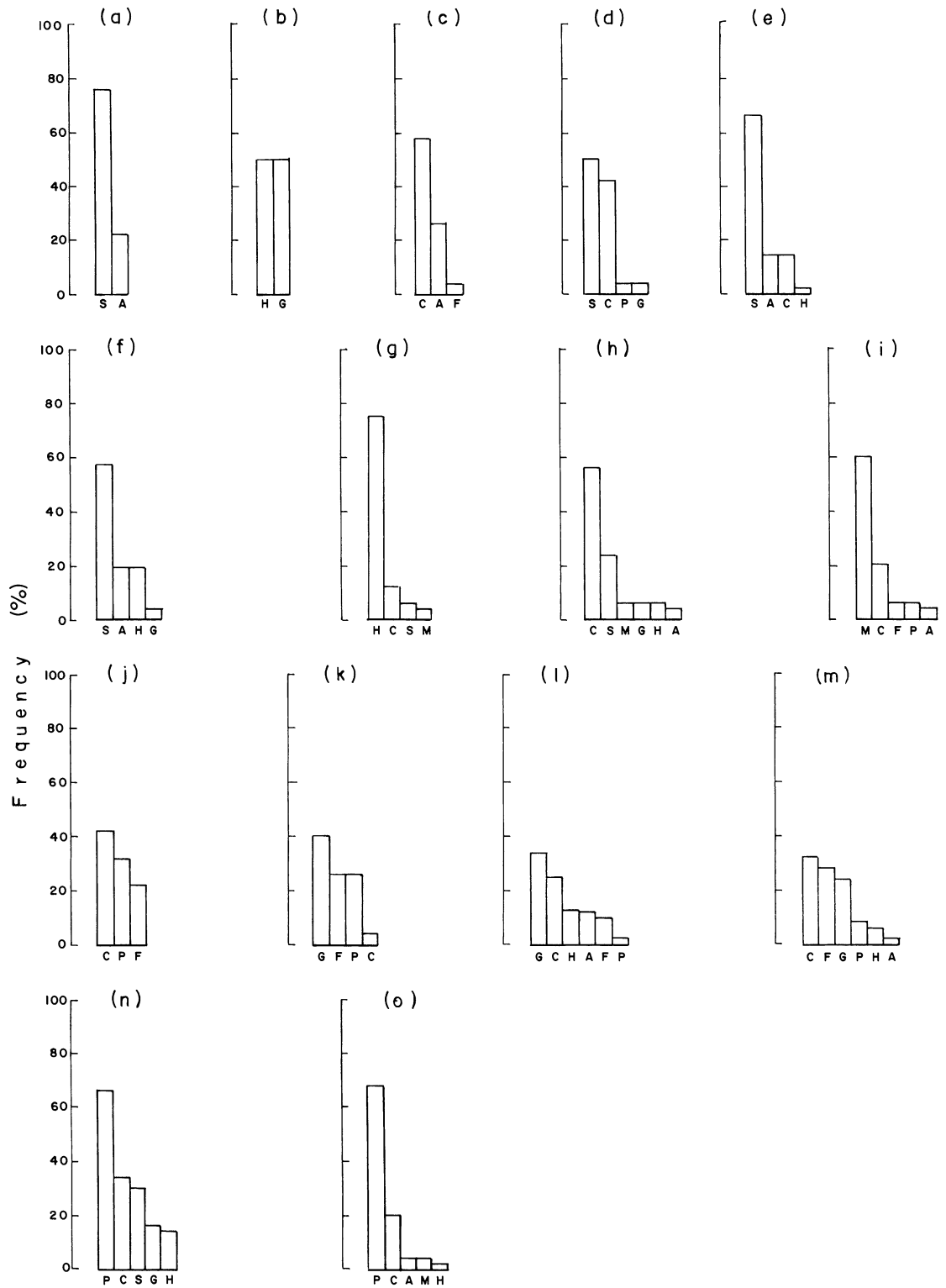


FIGURE 3. The mean percentage ( $\pm 1$  SE) of leaf area eaten for plants with (a) different life histories and (b) different growth forms.

and lianas), again differences were not statistically significant (Kruskal-Wallis test,  $P > 0.05$ ), although a much more marked order of herbs > lianas > trees emerged (Fig. 3b). The greatest contrast was between herbs and trees, and surprisingly, lianas were more similar to herbs than to trees. With the latter sole exception there is a tendency for more ephemeral plants (herbs and pioneers) to bear higher levels of damage than the more long-lived ones (trees and tolerants).

The 15 species selected for analysis of types of foliage

damage showed the occurrence of 8 major types (Table 1), including 2 types that are not strictly due to herbivores, although they may be somewhat related. These 2 types are physical damage (F) and pathogen damage (P). Damage type F can be caused by the fall of various objects (fruits, twigs) that tear the laminae, quite frequently in areas of the leaf where herbivores previously had caused some damage (e.g., holes, skeletonizations; found in *Lonchocarpus guatemalensis*, *Pterocarpus robrii*). Damage type P is defined by staining of the tissue (black, brown, yellow)



Types of insect damage

and its subsequent necrosis due to several pathogens. In several species of this forest (e.g., *Brosimum alicastrum*, *Pseudolmedia oxyphyllaria*, *Nectandra ambigens*), staining and necrosis occur where herbivores have (previously) damaged the tissue (R. Dirzo, pers. obs.). Several phytophagous insects are known to act as pathogen vectors by transmitting spores in their buccal parts (Kennedy 1951 in Crawley 1983). Together, these 2 types accounted for 24 percent of the total of damage types in the sample.

In relation to the damage types due directly to herbivores, several points are noticeable (Table 1). First, from the variety of types found, the major quantitative contribution is clearly due to the Lepidoptera (larvae), which cause four major damage types detected (C, H, S, and M). Second, no evidence was found of damage by herbivores other than insects; in particular, the absence of damage by vertebrates is noticeable. Additionally, most of the species in the sample showed a skewed distribution of types of damage (Fig. 4), i.e., one or two types were predominant. This tendency, however, was more marked in some species (e.g., *L. guatemalensis*, *Robinsonella mirandae*) than in others (e.g., *Costus villosissimus*, *N. ambigens*).

## DISCUSSION

The measurement of standing levels of damage must be taken with caution since they show only a static picture of herbivory, which may vary with time. However, the method adopted in this study (sampling the oldest leaves of each seedling) is likely to detect levels of herbivory that do reflect the damage accrued to a leaf through most of its life span, and the measurements may be comparable both intra- and interspecifically. An appropriate alternative is to mark individual leaves and follow their rates of herbivory through time (e.g., Coley 1980, 1983a and b). However, our method appeared to be convenient for a preliminary study demanding an extensive and relatively rapid survey of seedlings. The overall average levels of herbivory in the seedling community (10.5 and 9.3% on per-sample and per-species bases, respectively) are quite comparable to the standing levels found for the foliage of mature plants (trees) from several tropical localities. For example, at Barro Colorado Island (Panama), Leigh and Smythe (1978) found that trees lose 6–12 percent of their leaf area due to herbivores (mainly insects); Johnstone (1981) at Port Moresby (Papua New Guinea) found that herbivores (insects) consume approximately 7 percent of

TABLE 1. The types of damage, the herbivores responsible, and their relative frequency. Data are from a sample of 15 of the species studied.

Damage code	Damage description	Herbivore(s) responsible	Frequency (%)
C	Irregular chewing at edge of the leaves	Lepidoptera and Orthoptera	26.80
H	Holes <2 mm in diameter	Lepidoptera and Hemiptera	19.30
G	Holes ≥2 mm diameter	Coleoptera	17.8
A	Regular chewing at the edge of the leaves	Hymenoptera (Formicidae)	5.9
S	Skeletonization	Lepidoptera and Coleoptera	4.7
M	Miners	Lepidoptera and Diptera	1.0
P	Tissue staining and necrosis	Pathogens	8.9
F	Physical damage	—	15.9

the leaf area in extremely diverse mangrove communities; and Odum and Ruiz-Reyes (1970) measured herbivory on leaves collected from litter traps and found that 7 percent of the angiosperm leaf area was taken by herbivores. Interestingly, in a survey of trees made at Los Tuxtlas (including many of the species analyzed for the seedling community), the mean standing level of herbivory (mainly due to insects) was 8.9 percent (Dirzo 1984). Thus, the levels of herbivory on seedlings are strikingly similar to those of the trees of both the same and other tropical forests.

In contrast to these studies, Lowman (1984) carried out long-term observations of labelled leaves and found values of annual leaf area losses of 26, 22, and 14.6 percent in Australian cool, temperate, and subtropical rain forests, respectively. She also took discrete measurements and found that the latter method underestimated levels of damage by up to 5 times, with an overall mean discrepancy ratio of 2.5 for long-term discrete measurements. Long-term measurements are in progress for a number of seedlings at Los Tuxtlas, but results are not yet available.

The generality of the discrepancy found by Lowman (1984) must await similar comparative data obtained for other tropical communities. For the time being, if we take Lowman's overall discrepancy ratio as a correction factor for our measurements, the corrected figures would be 26.3

FIGURE 4. The frequency of occurrence of different types of insect damage (C, H, G, A, S, M, P, F) on the leaves of seedlings of 15 representative species (a–o) from Los Tuxtlas. The species are: (a) *Connarus schultesii*, (b) *Acalypha skutchii*, (c) *Pterocarpus robrii*, (d) *Allophylus compostachis*, (e) *Lonchocarpus guatemalensis*, (f) *Thinuia tomocarpa*, (g) *Robinsonella mirandae*, (h) *Costus spicatus*, (i) *Faramaea occidentalis*, (j) *Omphalea oleifera*, (k) *Costus villosissimus*, (l) *Psychotria faxlucens*, (m) *Nectandra ambigens*, (n) *Ampelocera botleii*, (o) *Brosimum alicastrum*. Letters coding the types of damage are described in Table 1.

TABLE 2. List of the species studied, their growth form, date of collection, and details of the levels of herbivory found.

Species (date of collection)	Growth form	Mean leaf area eaten (%)	Range area eaten (all leaves) (max. %)	C.V. (%)
<b>Pioneers</b>				
<i>Acalypha skutchii</i> (October 1983)	Shrub	24.00	57.0	64.8
<i>Bunchosia lindeniana</i> (May 1984)	Tree	18.80	48.0	109.6
<i>Bursera simaruba</i> (August 1984)	Tree	0.16	5.6	500.0
<i>Carica papaya</i> (February 1984)	Tree	7.60	35.0	118.4
<i>Cecropia obtusifolia</i> (November 1983)	Tree	5.93	38.0	162.0
<i>Ceiba pentandra</i> (July 1984)	Tree	9.15	42.7	148.4
<i>Costus spicatus</i> (April 1984)	Herb	8.20	39.4	120.0
<i>Costus villosissimus</i> (May 1984)	Herb	9.74	58.1	148.8
<i>Croton schiedeanus</i> (April 1984)	Tree	12.70	83.6	140.6
<i>Heliocarpus appendiculatus</i> (October 1983)	Tree	11.50	80.0	142.0
<i>Stemmadenia donnell-smithii</i> (November 1983)	Tree	4.88	43.0	229.0
<i>Solanum</i> sp. (July 1984)	Herb	9.18	58.6	128.2
<i>Schaueria calycobractea</i> (October 1983)	Shrub	14.20	55.2	96.6
<i>Trema micrantha</i> (July 1984)	Tree	3.17	60.20	347.0
<i>Trophis mexicana</i> (March 1984)	Tree	0.65	7.0	249.2
<i>Urera caracasana</i> (August 1984)	Tree	18.01	53.2	100.4
<b>Nomads</b>				
<i>Ampelocera bottlei</i> (August 1984)	Tree	9.11	54.8	148.1
<i>Brosimum alicastrum</i> (October 1983)	Tree	5.70	20.0	214.0
<i>Calophyllum brasiliense</i> (December 1983)	Tree	4.07	73.0	336.6
<i>Cordia alliodora</i> (November 1983)	Tree	24.16	75.0	91.2
<i>Cynometra retusa</i> (October 1983)	Tree	6.50	32.0	152.0
<i>Cupania dentata</i> (December 1983)	Tree	13.10	56.0	115.0
<i>Dussia mexicana</i> (January 1984)	Tree	18.86	58.0	97.0
<i>Guarea glabra</i> (June 1984)	Tree	18.30	59.0	91.2

TABLE 2. Continued.

Species (date of collection)	Growth form	Mean leaf area eaten (%)	Range area eaten (all leaves) (max. %)	C.V. (%)
<i>Inga</i> sp. (February 1984)	Tree	6.50	61.0	243.0
<i>Lonchocarpus guatemalensis</i> (November 1983)	Tree	3.21	18.0	175.0
<i>Omphalea oleifera</i> (January 1984)	Tree	19.80	81.0	109.6
<i>Pterocarpus robrii</i> (January 1984)	Tree	6.30	44.1	193.0
<i>Poulsenia armata</i> (October 1983)	Tree	1.78	43.0	376.0
<i>Pseudolmedia oxyphyllaria</i> (November 1983)	Tree	7.10	41.0	175.0
<i>Robinsonella mirandae</i> (July 1984)	Tree	7.04	87.6	231.4
<i>Spondias radlkoferi</i> (November 1983)	Tree	6.00	54.0	201.0
<i>Cymbopetalum baillonii</i> (October 1983)	Tree	3.80	39.0	201.0
<b>Shade-tolerants</b>				
<i>Allophylus campo-stachys</i> (October 1983)	Tree	8.20	65.0	201.0
<i>Apbellandra aurantiaca</i> (December 1983)	Tree	6.16	50.0	167.0
<i>Astrocaryum mexicanum</i> (May 1984)	Palm	13.50	57.5	120.0
<i>Chamaedorea</i> sp. (April 1984)	Palm	3.50	18.3	197.1
<i>Eugenia</i> sp. (February 1984)	Tree	9.08	65.0	299.5
<i>Faramea occidentalis</i> (October 1983)	Tree	12.89	59.0	135.5
<i>Hamelia longipes</i> (February 1984)	Tree	13.30	62.0	131.5
<i>Nectandra ambigens</i> (September 1983)	Tree	5.10	31.2	141.0
<i>Psychotria faxlucens</i> (October 1983)	Tree	3.76	10.3	158.0
<i>Psychotria simiarum</i> (April 1984)	Tree	0.97	14.4	355.0
<i>Orthion oblanceolatum</i> (December 1983)	Tree	6.42	51.0	188.0
<i>Rheedia edulis</i> (December 1983)	Tree	9.78	56.0	173.0
<i>Vatairea lundellii</i> (May 1984)	Tree	13.50	70.5	131.0
<b>Lianas</b>				
<i>Abuta panamensis</i> (March 1984)	Liana	13.00	51.8	125.5
<i>Connarus schultesii</i> (May 1984)	Liana	9.50	62.5	150.3

TABLE 2. *Continued.*

Species (date of collection)	Growth form	Mean leaf area eaten (%)	Range area eaten (all leaves) (max. %)	C.V. (%)
<i>Paullinia</i> sp. (June 1984)	Liana	10.44	68.0	185.8
<i>Salacia megistophylla</i> (January 1984)	Liana	9.80	63.5	167.3
<i>Strychnos tabascana</i> (March 1984)	Liana	8.60	40.0	173.2
<i>Thinouia tomocarpa</i> (June 1984)	Liana	13.90	64.9	140.3

and 22.2 percent leaf area losses on per-sample and per-species bases, respectively. These values are obviously much higher than those reported for some tropical sites (including Lowman's) but very close to those obtained by Coley (1982) for shade-tolerant species on Barro Colorado Island (21%) and by Lowman (1984) for cool-temperate and warm-temperate sites in Australia. Clearly, these recalculations must be taken with caution since measurements of trees (in particular) in somewhat dissimilar tropical forests may not be readily extrapolated to seedlings in truly tropical rain forests. For example, based on Coley's (1982) findings for Barro Colorado, a correction factor of 1.6 would be obtained; in this case the corrected figures for Los Tuxtlas would be 16.8 and 14.9 leaf area losses on per-sample and per-species bases, respectively; this discrepancy is considerably lower. No data appear to be available from other tropical seedling communities with which to compare the above. Two reports provide some general comparison. Dirzo (1984) surveyed the level of herbivory on 321 seedlings at Los Tuxtlas. He assigned leaves into 5 gross categories of damage and obtained results similar to ours (Fig. 1): the great majority of leaves were intact or very slightly damaged, and only a few showed damage above the level of 25 percent. In a study with plants of the same stratum as seedlings, Hendrix and Marquis (1983) measured damage on three species of ferns at La Selva, Costa Rica. They found average values of 9.9, 5.5, and 7.3 percent for each of the species—again, with very skewed distributions of percent damage and with the majority of fronds having  $\leq 10$  percent damage.

In addition to the similarity of herbivorous damage reported here to that reported by other workers, there is also a similarity of the herbivores found to be responsible for the damage. Insects (in our particular case, Lepidoptera) are the main consumers of the foliage.

The predominant role of insects as foliage consumers has been established for several tropical sites (*e.g.*, Leigh

& Smythe 1978, Janzen 1981, Dirzo 1984), but this conclusion has been based mostly on the study of mature plants and not seedlings or herbs of the forest understory. That insects should also play a predominant role at this level is somewhat surprising, for other folivores, in particular ground-dwelling vertebrates (tapirs, deer, peccaries), also could be expected to be important consumers. Since the vertebrate fauna of Los Tuxtlas is quite pauperized (due in part to excessive contemporary hunting), the generality of this finding cannot yet be assessed. Another possibility is that our sampling method may have overlooked damage by vertebrates leading to whole leaf consumption; however, observations of individually marked seedlings and leaves for over 2 yr at Los Tuxtlas (R. Dirzo, pers. obs.) have also failed to detect any substantial degree of damage by herbivores other than insects (and pathogens). These long-term studies also show that whole-leaf consumption (by whatever agent) is minimal.

Even though the levels of herbivory found in the present study were concentrated on the lower end of the distribution, some degree of intra- and interspecific variation occurred. At the intraspecific level, the coefficients of variation (see Table 2) indicate that some species do show more variation than others, but no consistent patterns have been detected as yet. Since all the seedlings for a given species were collected at about the same time and within the same visibly homogeneous area, we cannot invoke spatial or temporal heterogeneity (although a detailed phenological study is needed to clarify the effects of temporal heterogeneity). The proximal and/or ultimate explanations responsible for this level of intraspecific variation warrants further study (see Coley 1983b). In relation to the levels of interspecific variation, Feeny (1976) and Rhoades and Cates (1976) have advanced a comprehensive theory that the evolution of antiherbivore mechanisms has occurred as a consequence of the likelihood of discovery by herbivores (the plant's apparency) and the relative cost of defense. In their hypothesis, early successional should be unapparent to herbivores due to their relative unpredictability in space or time. Associated with escape via unapparency, these plants allocate little of their resources to defense. The opposite is true for later successional (apparent plants). Several workers (Cates & Orians 1975; Coley 1980, 1983a; Hartshorn 1980) have found some evidence of a greater susceptibility to herbivory in early successional than in late successional.

In the present study, however, no significant differences were found in the levels of herbivory among pioneers, nomads, and shade-tolerants, nor among herbs, lianas, and trees, although putatively unapparent plants (herbs and pioneers) showed a marked tendency to be more damaged. These results suggest that because of differential apparency (or other alternative mechanisms), plants with different life histories are similarly successful (or unsuccessful) in escaping herbivory. This result would be ex-

pected if early and late successional rely on different, but equally effective, antiherbivore strategies that resulted from natural selection. However, another likely explanation is that there are consistent differences in leaf life times (pioneers < nomads < tolerants), which would mean that similar standing levels of damage could result from fast rates of herbivory on short-lived leaves, or from slow rates on long-lived leaves.

What are the proximal or ultimate causes underlying the levels of herbivory? Which herbivores are responsible? What is the expected degree of variation in herbivory on

seedlings for tropical forests? Answers to such questions warrant further study and careful attention by tropical biologists.

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