

## INTRASPECIFIC VARIATION IN HERBIVORY ON TWO TROPICAL TREE SPECIES<sup>1</sup>

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**Abstract.** Levels of herbivory on young and mature leaves were determined for two tree species, *Trichilia cipo* (Meliaceae) and *Cecropia insignis* (Moraceae), in a lowland rain forest of Panama. Saplings of both species were studied in light gaps, and in addition, *Trichilia* was studied in the understory. Rates of leaf damage by insects were measured on marked plants during four 3-wk sample periods conducted at 5-mo intervals. Mature leaves of *Cecropia* suffered average damage rates that were five times greater than those suffered by *Trichilia*; the reverse was true for young leaves. Patterns of intraspecific variation in herbivory on mature leaves were similar for the two species, despite differences in life history, habitat, defensive characteristics, and levels of damage. Variation among individuals at any one sample period was high. Damage levels during sequential samples were not significantly correlated within an individual but were highly variable. For each sample period, a different group of individuals (with one exception) comprised the 20% most heavily grazed. These patterns of herbivory are discussed with respect to seasonal effects, possible causal mechanisms, and implications for escape from herbivores and selection of defenses.

**Key words:** *Cecropia*; herbivory; intraspecific variation; Panama; temporal distribution; treefall gaps; *Trichilia*; tropical forest; understory.

### INTRODUCTION

The importance of herbivory as a selective force in plant evolution has received considerable attention (Feeny 1976, Rhoades and Cates 1976). Intraspecific variation in levels of herbivory affects the success of individual plants and may therefore influence the evolution of antiherbivore characteristics. The degree to which differences in rates of herbivory on individual plants reflect differences in defensive properties will influence the direction and speed of natural selection on these defenses. Intraspecific variation in herbivory may also affect the survival or reproductive success of individual plants, thereby changing the population structure of present and subsequent generations. Experimental manipulations of vegetation density and diversity and examinations of defenses have been undertaken to demonstrate mechanisms responsible for differential herbivory on individuals within a population (e.g., Pimentel 1961a, b, Jones 1962, Root 1973, Rhoades 1977). However, the extent of variation in levels of herbivory between individuals in natural populations is not well documented.

The goals of the present study were to quantify two components of intraspecific variation in leaf damage: (1) the amount of variation among individuals in the population at any one period, and (2) the temporal variation in rates of damage to a particular individual. The first question examines the evenness of damage distribution and the magnitude of the differences, since these may influence the potential for natural selection. The second question examines the effectiveness of escape from herbivores (*sensu* Feeny 1976) by compar-

ing the probability that an individual will avoid damage in the short term with probabilities averaged over longer periods. The constancy of damage to a plant through time also points to seasonal effects and may suggest the types of mechanisms responsible for the distribution of herbivory.

Intraspecific variation of naturally occurring herbivory was examined for two tropical canopy tree species with different life histories and habitat requirements. *Cecropia insignis* (Moraceae) is fast growing and only colonizes existing light gaps made by fallen trees. It experiences high levels of grazing, probably due primarily to specialist herbivores (Coley 1981, 1983). Plants were examined before they started to produce protein-rich Müllerian bodies, which attract protective ants. *Trichilia cipo* (Meliaceae) is slow growing and occurs in both the shaded forest understory and in light gaps. *Trichilia* has low rates of grazing by insect herbivores and appears well defended (Coley 1981, 1983). It has higher concentrations of fiber and phenolic compounds, lower nitrogen and water contents, and tougher leaves than *Cecropia*. Since the spatial distribution and the defensive systems of these two species are different, theories of plant/herbivore interactions (Root 1973, Feeny 1976, Rhoades and Cates 1976) predict that *Trichilia* should have a more even distribution of damage among individuals over time.

### METHODS

The investigation was carried out on Barro Colorado Island in the lowland rain forest of Panama. Descriptions of the vegetation can be found in Knight (1975), Croat (1978), and Leigh et al. (1983). Individuals of *Cecropia* and *Trichilia* were studied in 20 light gaps in the mature forest. Light gaps ranged in size from 100

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TABLE 1. Rates of herbivory on young and mature leaves on *Trichilia cipo* and *Cecropia insignis*. Herbivory is measured as the percent leaf area eaten per day for a 3-wk sample period. Annual rates are the average of all sample periods weighted for an 8-mo wet season. SD = standard deviation, CV = coefficient of variation, Skew = skewness, Kurt = kurtosis,  $n$  = number of plants.

Season	Mature leaves						Young leaves					
	Mean (%/d)	SD	CV (%)	Skew	Kurt	$n$	Mean (%/d)	SD	CV (%)	Skew	Kurt	$n$
<i>Cecropia</i>												
Dry 1979	0.04	0.09	263	3.79	14.8	16	0.04	0.10	259	3.73	14.2	15
Early wet 1979	0.21	0.61	292	3.89	15.9	25	0.03	0.09	328	4.62	2.22	26
Late wet 1979	0.08	0.21	252	4.40	21.5	33	0.27	0.91	334	3.84	14.5	30
Annual	0.12	0.25	220	3.79	16.9	43	0.18	0.74	401	4.84	23.5	46
<i>Trichilia</i> (sun)												
Dry 1979	0.01	0.03	341	3.91	15.6	17	0.84	0.89	106	0.38	-1.82	10
Early wet 1979	0.02	0.04	279	4.06	12.4	22	0.86	1.33	154	2.07	4.49	13
Early wet 1980	0.11	0.46	422	4.92	25.0	29	0.66	0.96	146	1.48	0.73	29
Late wet 1979	0.02	0.04	259	3.36	11.0	29	1.35	1.88	139	1.17	-0.46	18
Annual	0.03	0.14	399	5.65	32.7	35	0.85	1.07	126	1.75	3.26	43
<i>Trichilia</i> (shade)												
Dry 1979	0.00	0.00	332	3.32	11.0	11	0.39	0.36	9			3
Early wet 1979	0.02	0.08	352	4.54	20.9	22	0.88	0.73	84	0.37	-0.55	10
Early wet 1980	0.03	0.11	430	5.11	26.3	27	0.44	0.67	151	1.73	1.74	23
Late wet 1979	0.03	0.12	431	5.06	25.7	26	1.36	1.99	147	1.50	0.74	10
Annual	0.02	0.06	258	3.07	8.66	29	0.88	1.10	124	2.16	5.80	31

to 800 m<sup>2</sup> and were  $\approx$  1–2 yr old. An additional population of *Trichilia* was followed in the understory of the mature forest. Plants were between 0.75 and 1.5 m tall at the beginning of the study.

The size and species composition of each light gap was determined. The saplings of *Cecropia* and *Trichilia* per gap were counted; numbers of 45 of the other most common pioneer and persistent tree species were also determined.

Rates of herbivory were measured on marked young and mature leaves. Leaves were defined as young from the time they emerged from the bud until they were completely expanded and had adult characteristics. Marked mature leaves were fully developed but not senescent. Herbivory was quantified by determining the total leaf area and damaged portions at time zero and again 3 wk later. Grazing rates were expressed as the percentage of leaf area damaged per day, which corrects for absolute area changes in an expanding young leaf (Coley 1980). For statistical analyses using parametric techniques, the data were transformed to stabilize the variances (Snedecor and Cochran 1967, Bliss 1970):  $\ln[(1000 \times \% \text{ leaf area eaten per day}) + 1]$ . Measures of dispersion (e.g., skewness, kurtosis, and variance) were computed from the nontransformed data.

Rates of herbivory were determined in the dry season (February 1979), early wet season (June 1979), and late wet season (October 1979). For individuals of gap and understory *Trichilia*, measurements were also taken in June 1980.

For individuals of *Trichilia* rates of herbivory were measured on eight leaves or  $\approx$  14% of the mature leaves

present each sample period. *Trichilia* leaves live 32 mo (Coley 1983), so that grazing measures were taken from essentially the same population of leaves. On *Cecropia*, which has fewer, larger leaves, three leaves per plant were measured, equivalent to 42% of the average number of mature leaves. For both species, grazing was quantified on  $\approx$  60% of all young leaves emerging on a plant each sample period. Since a high proportion of the leaves on a plant were sampled, estimates of between-plant differences in herbivory are not due to within-plant variation.

Plant height was measured at 3-mo intervals from December 1978 until December 1979 for *Cecropia*, and until July 1980 for *Trichilia*. Growth rates for various time periods were calculated as the absolute height increment: (final height – original height). When this is plotted against original height, the slope is indistinguishable from zero ( $P < .05$ , *Cecropia* slope = -0.009, *Trichilia* sun slope = -0.002, and *Trichilia* shade slope = -0.0002). Therefore growth, as defined here, is independent of original height. The number of young leaves present on the plant each sample period as well as the total annual production of leaves was also determined.

## RESULTS

### *Variation in herbivory within populations: mature leaves*

Seasonal and annual estimates of herbivory are presented for young and mature leaves of each species (Table 1). On the average, mature leaves of *Cecropia* are grazed at a rate four to six times greater than those of *Trichilia* ( $P < .05$ , Mann-Whitney  $U$ ). This is con-

sistent with the general patterns seen for pioneer and persistent species (Coley 1981, 1983). There is no significant difference in the amount of grazing between *Trichilia* plants growing in the sun and those in the shade ( $P > .3$ , Mann-Whitney  $U$ ). For all populations, the levels of herbivory are lower in the dry season than in the early or late wet season ( $P < .05$ , Mann-Whitney  $U$ ). Grazing on *Trichilia* in the early wet season of 1970 was not significantly different from that in 1980, although rates were slightly higher in 1980.

Despite seasonal and species differences in average levels of herbivory on mature leaves, the distribution of damage among plants in all populations is comparable (Table 1 and Fig. 1: mature leaves). The variation in herbivory among individuals is high for *Cecropia* and for both sun and shade populations of *Trichilia*. Coefficients of variation average  $>250\%$  (Table 1: mature leaves). Grazing rates in all populations are significantly positively skewed ( $P < .01$ ); thus, the modal individual suffers less damage than the mean. The degrees of kurtosis in all populations are also similar, indicating a significant ( $P < .01$ ) excess of plants near and far from the mean. In the analysis, pooling *Trichilia* plants from the gap and understory does not change these patterns. The population of *Trichilia* in light gaps, however, appears more variable for the annual herbivory measures than the population in the shade.

Seasonal and annual measures of the intraspecific distribution of damage on mature leaves all show heavily grazed outliers with levels of damage much higher than the rest of the population (Fig. 1 and Appendix: mature leaves). However, individuals that are grazed much less than the population median, and might therefore be considered to have escaped, are infrequent.

The effects of spatial distribution of individuals and the identity of neighbors on rates of herbivory were examined for plants growing in light gaps. *Trichilia* and *Cecropia* have similar densities and spatial distributions within gaps. Both species are common, with an average density of two plants per gap for *Cecropia* and three for *Trichilia*. They also have equivalent distributions as measured by Lloyd's (1967) index of patchiness (6.4 and 4.4, respectively). Species composition in the 20 gaps was not related to rates of herbivory for young or mature leaves of either species. Densities and absolute numbers of conspecifics, pioneers, persistents, and all species combined are not significantly correlated ( $P > .05$ ) with herbivory. The number of different species in each of the above categories also shows no correlation with herbivory.

#### Variation in herbivory within populations: young leaves

Young leaves are grazed significantly more than old ones ( $P < .05$ , Mann-Whitney  $U$ ), with particularly heavy grazing on young leaves of *Trichilia* (Table 1

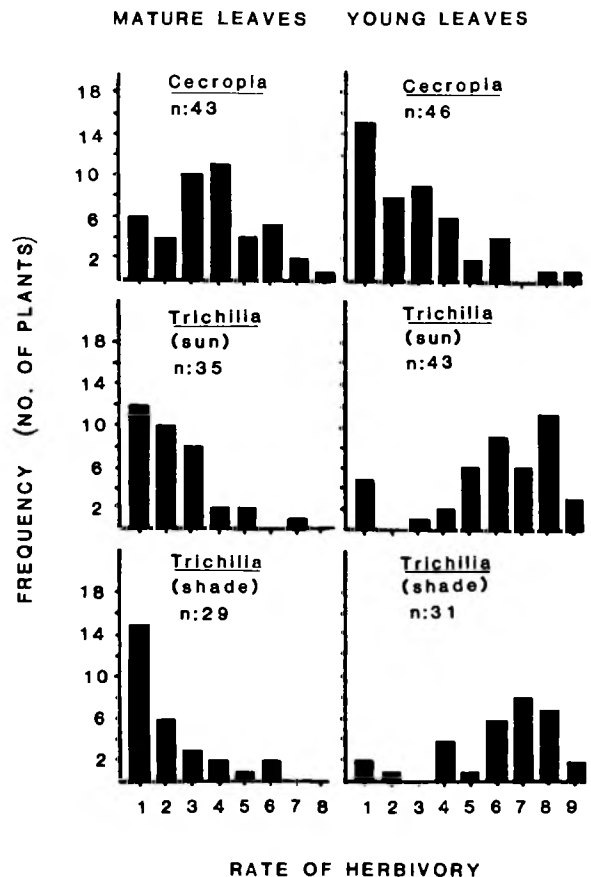


FIG. 1. Log-transformed rates of herbivory on *Cecropia* and on understory and light-gap populations of *Trichilia*. Rates are the average for each plant of all sample periods computed as:  $\ln[(1000 \times \% \text{ leaf area eaten per day}) + 1]$ .

and Fig. 1: young leaves). Rates of herbivory are similar for *Trichilia* in sunny and shaded sites ( $P > .4$ , Mann-Whitney  $U$ ). Although seasonal differences in herbivory are not significant, in all three populations damage is lowest in the dry season and highest in the late wet season. There is no significant difference between herbivory in the early wet seasons of 1979 and 1980.

The intraspecific distribution of damage on young leaves differs between *Trichilia* and *Cecropia* (Table 1 and Fig. 1: young leaves). Young *Cecropia* leaves show greater between-plant variation in damage by all measures of dispersion than any other class of leaves (Table 1). This may be partially attributed to the fact that *Cecropia* leaves have a shorter period of vulnerability to herbivores; they take only 18 d to become fully expanded from the bud compared to 49 d for young *Trichilia* leaves. The high intraspecific variation probably is not due to the seasonal distribution of young leaves, since *Cecropia* has a much more even production through time than *Trichilia*. The coefficient of variation for the number of young leaves present on

an individual in each of six sample periods was used as a measure of the synchrony of leaf production within plants. For individuals of *Cecropia*, this averages 15% as compared to 169% for *Trichilia*. The synchrony in leaf production among individuals within a species was quantified as the coefficient of variation for the percentage of plants with young leaves at eight periods during the year. Since virtually 100% of the *Cecropia* individuals have young leaves even in the dry season, the coefficient of variation is only 3%. This contrasts with *Trichilia*, which has a within-species coefficient of variation of 37%, more than 10 times the value for *Cecropia*. In addition to showing both within-plant and within-species synchrony of leaf emergence, the major peak for *Trichilia* is in the early wet season, which coincides with the forest-wide peak in production (Leigh and Smythe 1978).

#### *Temporal variation in herbivory within individuals*

Relative levels of damage on individual plants are not constant over time for young or mature leaves of either species (see Appendix). Plants which are heavily grazed during one sample period may completely escape further damage during the next. For each sample period, a different group of individuals (with one exception) comprised the 20% most heavily grazed. An ANOVA on log-transformed grazing rates for each species shows a significant effect ( $P < .01$ ) of sample period and the interaction between plants and sample period for leaves of both ages. If individuals are consistently well defended or poorly defended against herbivores, one would expect positive correlations between the rate of grazing on a plant at one time with that at any other time. However, only 3 of the 65 possible correlations are significant ( $P < .05$ ), and less than half are positive. These patterns of noncorrelation are obtained whether the grazing rate per plant is expressed as the grazing rate per day, whether it is log transformed, or whether it is standardized within a season by a  $z$ -transformation. An individual's position relative to the population mean is thus highly variable, changing in each sample period.

Young and mature leaves on the same plant are not grazed to similar degrees (see Appendix). For a given season, the young leaves may be eaten more than the population mean and the mature leaves untouched, while in the following season, the reverse may be true. There are no significant correlations between herbivory on young and mature leaves on the same plant for any sample period. There are also equal numbers of positive and negative correlations. This suggests that different herbivores are attacking leaves of different ages.

If plant defenses were induced as a response to herbivory, we would expect damage levels at some later period to be reduced, assuming herbivore pressure re-

mained essentially constant. However, none of the correlations between grazing rates in one sample period and those in any of the following ones is significant for either young or mature leaves ( $P > .05$  in all cases; see Appendix). In addition, there are equal numbers of positive and negative correlations between grazing on young leaves and damage in the previous sample period to either young or mature leaves. For mature leaves of *Trichilia* and *Cecropia*, seven of the eight correlations were negative ( $P < .05$ , chi-square), suggesting that there may be a weak effect of defense induction.

#### *Growth and herbivory*

To determine the influence of herbivory on the success of individual plants, rates of growth and mortality were compared with grazing damage. Annual growth rates of surviving individuals (see Appendix) are not significantly correlated ( $P > .05$ ) with annual rates of herbivory for young or mature leaves in either species. There are also no significant correlations between rates of grazing in any season and growth in the following 3 mo. However, for mature leaves, grazing in the dry season is negatively correlated (NS) with growth rate estimates in 10 of the 12 3-mo sample periods for the following year ( $P < .05$ , chi-square). Furthermore, growth is inversely related to herbivory when values are averaged over longer time periods. The combined grazing rates in the dry and early wet seasons are negatively correlated, although not significantly, with growth rates during the next year for *Trichilia* populations and the following 6 mo for *Cecropia*.

Rates of herbivory are negatively correlated with plant survival. No *Trichilia* died during the study, but 15 of the 50 *Cecropia* died. Dry-season grazing rates were significantly higher ( $P < .05$ , Kolmogorov-Smirnov) on *Cecropia* plants that died than on those that survived the next 3 mo. Also, plants that died any time within the following year had suffered higher dry-season grazing on mature leaves ( $P = .07$ , Kolmogorov-Smirnov). Grazing during other seasons was not related to mortality.

#### DISCUSSION

Patterns of intraspecific variation are similar for *Trichilia* and *Cecropia* despite differences in life histories, defensive characteristics, and levels of leaf damage. *Cecropia* exhibits many of the characteristics (Coley 1981, 1983) that are hypothesized for species that rely primarily on escaping discovery by herbivores and not on effective physical or chemical defenses (Feeny 1976, Rhoades and Cates 1976). *Trichilia*, on the other hand, resembles unapparent species (sensu Feeny 1976), so one would expect a more even distribution of damage among individual plants. However, patterns of intraspecific variation do not support these predictions. For both species, variation in her-

bivory between plants at any one sample period is high, and rates of damage to a particular individual are not constant with time.

The density of conspecifics and general diversity of the surrounding vegetation have been shown to influence levels of herbivory. In experimental manipulations, increasing vegetational diversity is correlated with decreased damage levels from herbivores (Pimentel 1961*b*, Tahvanainen and Root 1972, Root 1973, Risch 1979, Bach 1980). Effects of plant density are less clear, with some results supporting a resource concentration hypothesis (Cromartie 1975, Ralph 1977, Thompson 1978) and others suggesting satiation of herbivores at high plant densities (Pimentel 1961*a*, Way and Heathcote 1966, A'Brook 1973, Jones 1977, Futuyma and Wasserman 1980). Few studies have examined these aspects in natural communities (but see Thompson 1978, Futuyma and Wasserman 1980, Rausher and Feeny 1980). The present study found no effect of species composition in gaps on herbivore damage. Furthermore, *Trichilia* exhibits equivalent patterns of herbivory in both understory and light gaps which differ dramatically in terms of microclimate, species composition, and density (Rubinoff 1974, Brokaw 1980, Leigh et al. 1983).

The relative levels of damage on an individual are not predictable or constant but fluctuate over time without detectable pattern. There are no consistent positive trends in correlations between grazing rates in sequential sample periods for either *Cecropia* or *Trichilia*. We might expect this variable pattern of damage if a given set of defensive properties was not consistently effective throughout the seasons. Herbivore populations fluctuate seasonally and annually (Lawton 1976, Wolda 1978), so it seems possible that defenses which are effective against the array of herbivores present at one time may not be as effective against those present at another. Correlations between short-term measures of damage and various plant or leaf characteristics may therefore be misleading. Fluctuations in the type and intensity of herbivore pressure could be important in selecting for seasonal changes in defenses or in maintaining a diversity of plant defenses in the population (Jones 1962, 1972, Dement and Mooney 1974, Rockwood 1974, Cooper-Driver and Swain 1976, Cooper-Driver et al. 1977, Sturgeon 1979, Janzen et al. 1980).

Induction of chemical defenses following grazing has been shown for several species (Hillis and Inoue 1968, Thielges 1968, Deverall 1972, Green and Ryan 1972, Ingham 1972, Russel and Berryman 1976, Albersheim and Valent 1978, Bhaskaran and Kandaswamy 1978, Reuveni and Cohen 1978, Ryan 1978, Rhoades 1979) and in some cases may be responsible for temporal changes in a plant's susceptibility to herbivores (Baltensweiler et al. 1977, Haukioja and Niemela 1979, Bryant 1981). There is no evidence to suggest that

*Trichilia* and *Cecropia* show defense induction, although it is possible that induction and relaxation of defenses occur on a shorter time scale than the 3 mo-interval between sample periods. I suggest that inducibility may be selectively advantageous in a short-lived plant species where rapid growth or large reproductive output is critical. Defense induction may also be more common in species which occur in low-diversity stands with large numbers of conspecifics and in species which have several major specialist herbivores. The diversity of both herbivores and trees in tropical lowland forests such as Barro Colorado Island would probably make "tracking" of herbivore populations difficult and would reduce the advantage of defense induction. Perhaps for these reasons, we see little evidence of induction in either young or mature leaves of *Trichilia* and *Cecropia*.

For young leaves of both species, herbivory is lowest in the dry season, slightly higher in the early wet season, and peaks in the late wet season. This may be owing to a combination of leaf availability and herbivore abundance. Herbivore density is lowest in the dry season, increases with the onset of the rains, and declines throughout the remainder of the wet season (Leigh and Smythe 1978, Wolda 1978). Young leaves are approximately five times more abundant in the early wet season (Leigh and Smythe 1978), which may have the effect of satiating available herbivores (McKey 1974). Thus, when both herbivores and young leaves are common, as in the early wet season, or when both are scarce, as in the dry season, levels of herbivory are moderate. In the late wet season, when greatest rates of damage occur, availability of young leaves is very low, but herbivore populations are still relatively high. The patterns of leaf emergence at the population or community level therefore appear to influence overall rates of herbivory.

Mature leaves of both species are also grazed less in the dry season than in the wet season. The low herbivore populations at this time (Leigh and Smythe 1978, Wolda 1978) are probably the major reason for decreased damage; however, it is possible that seasonal differences in defenses may also contribute. Preliminary data on mature leaves indicate that concentrations of nitrogen and water for both species are lower in the dry season (P. D. Coley, *personal observation*). In addition to reduced nutritive value, *Cecropia* has significantly higher concentrations of phenolic compounds in the dry season (P. D. Coley, *personal observation*).

In this study, the lack of constancy of damage to plants over time implies that individuals are not consistently avoiding damage or escaping from certain herbivores (*sensu* Feeny 1976). Only infrequently are individuals grazed much less than the rest of the population, and this relief from herbivory is short lived. If damage levels were averaged over a plant's lifetime,

intraspecific variation would probably show a further reduction. It is therefore risky to make assumptions concerning escape based on short-term samples of herbivory.

Although plants do not appear to escape discovery by herbivores consistently, short-term escape of individuals could reduce the mean level of grazing for the population as a whole. If at any one time herbivores have difficulty finding all plants, their populations would be maintained at a reduced level. Escape in this time scale may not have a significant effect on long-term intraspecific variation in grazing, but lower rates of herbivory could potentially influence selection for lowered defenses.

The significance of herbivory as a selective agent depends, in part, on intraspecific variation in damage and on a negative relationship between damage and plant reproductive success. First, for both *Trichilia* and *Cecropia*, intraspecific variation in damage is high, as indicated by large coefficients of variation and significant levels of skewness and kurtosis. Second, although a causal relationship was not explicitly demonstrated, plant survivorship and growth were inversely related to rates of herbivory. However, the temporally inconsistent pattern of herbivory on an individual suggests that there is a complex interaction of factors and that levels of grazing are not simply associated with plant defenses or with species composition and density of neighbors. Instead, the highly variable component of damage may be due to differential effectiveness of defenses against changing herbivore populations or to insect grazing without regard to an individual plant's characteristics. Therefore, to evaluate the influence of herbivory on plant success fully, or even to describe the timing and distribution of grazing damage accurately, one must consider both the intraspecific variation and the lack of temporal constancy in herbivory.

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## APPENDIX

Annual growth rates and seasonal rates of herbivory on individual plants of *Cecropia* and sun and shade populations of *Trichilia*. Herbivory is expressed as the percent leaf area eaten per day, and growth as the absolute change in height (cm) over 1 yr. Plants are included if at least two seasons of herbivory data exist. Missing values are because of plant loss or lack of leaves in a particular age-class.

Species	Plant no.	Herbivory: mature leaves				Herbivory: young leaves				Growth
		Dry 1979	Early wet 1979	Late wet 1979	Early wet 1980	Dry 1979	Early wet 1979	Late wet 1979	Early wet 1980	Height change (cm)
<i>Cecropia</i>	1	0.001	0.002	0.236		0.000	0.003	0.021		103
	2	0.003	0.010	0.058		0.000	0.464	0.015		123
	3	0.007	0.000	0.020		0.002	0.001	0.004		36
	4	0.045	0.005	0.007		0.042	0.008	0.011		160
	5	0.007	0.001	0.078		0.011	0.002			133
	6	0.000	0.007	0.054		0.381	0.008			47
	7	0.000	0.034	0.005						87
	8	0.012	0.068	0.038						-14
	9	0.001	0.022			0.000	0.022			44
	10	0.000	0.365			0.001	0.001			95
	11	0.001	2.834			0.028				180
	12		0.013	0.022		0.018	0.023	0.018		11
	13		0.000	0.029			0.000			196
	14		0.015	0.010			0.000	0.001		126
	15		0.010	0.004			0.012	0.138		130
	16		0.001	0.048			0.002	0.008		166
	17		0.040	0.001			0.121	0.270		216
	18		0.027	1.158			0.001			176
	19		0.005	0.004			0.004	0.001		230
	20		0.024	0.022			0.007	0.006		64
	21		0.001	0.304			0.000			66
	22			0.000	0.005		0.036	0.005		46
	23			1.270	0.005		0.002	0.011		
<i>Trichilia</i> (sun)	1	0.000	0.000	0.043	0.002	1.449		3.889	0.694	14
	2	0.000	0.002	0.002	0.626	1.000			0.378	78
	3	0.001	0.009	0.027	0.000	1.548		0.087	2.460	75
	4	0.000	0.191	0.001	0.000	0.000	2.100		0.000	51
	5	0.000	0.011	0.000	0.000		1.996		1.939	7
	6	0.000	0.025	0.144	0.000		0.006	0.659	2.362	5
	7	0.000	0.055	0.000	0.002				3.099	32
	8	0.006	0.000	0.006	0.002		0.094		2.109	45
	9	0.000	0.000	0.000	0.002	0.000			0.108	44
	10	0.000	0.000	0.007	0.000				0.000	12
	11	0.023	0.000	0.000	0.000	0.128		0.070	2.536	52
	12	0.000	0.000	0.000	0.014	2.167				68
	13	0.122	0.000	0.003	0.000	2.000			0.000	17
	14		0.000	0.033	0.000		4.546		0.006	64
	15		0.000	0.188	2.378		0.007			36
	16		0.008	0.002	0.001		0.032	0.281	0.097	32
	17		0.006	0.002	0.000		0.920		0.078	20
	18	0.002	0.000		0.000	0.034			0.520	9
	19	0.000		0.000	0.000			0.189	0.374	42
	20		0.000	0.002	0.036		0.000			60
<i>Trichilia</i> (shade)	1	0.000	0.012	0.048	0.000		1.756	0.015	0.229	15
	2	0.000	0.007	0.000	0.028	0.400				5
	3	0.000	0.000	0.000	0.003		1.110			2
	4	0.000	0.000	0.005	0.599		1.140		0.155	6
	5	0.000	0.001	0.001	0.000	0.344			0.075	0
	6	0.000	0.002	0.009	0.000			0.676		0
	7	0.000	0.002	0.016	0.007		0.046		0.307	3
	8	0.000	0.001	0.000	0.000		0.000		0.078	10
	9	0.000	0.001	0.002	0.001				0.031	12
	10	0.000	0.000	0.003	0.001		0.626		0.000	-2
	11	0.000	0.001	0.001	0.002	0.412		0.007	1.200	1
	12		0.006	0.000	0.000			0.280	0.008	3
	13		0.024	0.007	0.058		1.077		0.414	7
	14		0.048	0.001	0.002				0.003	0
	15		0.000	0.000	0.010				0.032	2
	16		0.000	0.003	0.003		0.827		0.088	-2
	17		0.000	0.002	0.001				0.000	2
	18		0.000	0.681	0.000		1.706			8
	19		0.024	0.005	0.004			5.000		23