

HERBIVORY AND DEFENSIVE CHARACTERISTICS OF TREE SPECIES IN A LOWLAND TROPICAL FOREST¹

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Abstract. Rates of herbivory and defensive characteristics of young and mature leaves were measured for saplings of 46 canopy tree species in a lowland tropical rain forest (Barro Colorado Island, Panama). Grazing rates were determined in the field for sample periods in the early wet, late wet, and dry seasons. Leaf properties such as pubescence, toughness, water, protein, fiber, and phenolic contents explained over 70% of the variation among plant species in the rates of herbivory on mature leaves. Leaf toughness was most highly correlated with levels of herbivory, followed by fiber content and nutritive value. Phenol content and phenol:protein ratios were not significantly correlated with damage.

Mature leaves of gap-colonizing species were grazed six times more rapidly than leaves of shade-tolerant species. Gap-colonizers have less tough leaves, lower concentrations of fiber and phenolics, higher levels of nitrogen and water, shorter leaf lifetimes, and faster growth rates than do shade-tolerant species. Gap-colonizers did not escape discovery by herbivores to any greater extent than shade-tolerant species, as measured by the spatial distribution of plants or by the intraspecific distribution of herbivore damage under natural or experimentally manipulated conditions.

In 70% of the species, young leaves suffered higher damage levels than mature leaves. Although young leaves are more nutritious and less tough and fibrous, they have two to three times the concentrations of phenols. The temporal appearance of young leaves was not correlated with the distribution of herbivory among individuals of a species.

Interspecific patterns of defense mechanisms are discussed in terms of current theories of plant apparency, and an alternative model for the evolution of plant defenses is presented.

Key words: *fiber; herbivory; life history; Panama; phenolics; plant defenses; plant growth; spatial distribution; tannins; temporal distribution; treefall gaps; tropical forest.*

INTRODUCTION

Herbivory in natural communities can be high, reducing growth and reproduction of individual plants, and influencing competitive outcomes and community composition (Harper, 1969, Kulman 1971, Rockwood 1973, Morrow and LaMarche 1978, Springett 1978, Wolda and Foster 1978, Windle and Franz 1979, Rausher and Feeny 1980). However, it has only recently become accepted that plants possess a variety of defensive mechanisms against herbivores (Fraenkel 1959, Sondeheimer and Simeone 1970, Harborne 1972, Rosenthal and Janzen 1979). The ubiquity and diversity of plant defense mechanisms have prompted questions concerning their relative effectiveness and cost and the nature of the selective forces influencing their evolution. The distribution of defenses among species and plant tissues has both ecological and evolutionary significance for feeding patterns and population dynamics of herbivores, as well as for the success of individual plant species in different communities. The goal of this research was to determine general patterns of herbivory and plant defensive characteristics for a range of tree species in a single natural community.

A comprehensive theory concerning optimal patterns of plant defense has emerged primarily from the

work of Feeny (1976) and Rhoades and Cates (1976). They state that the evolution of different antiherbivore mechanisms and their allocation within a plant have been in response to the risk of discovery by herbivores, the cost of defense, and the value of the plant part. They suggest that young leaves and early successional plants are difficult for herbivores to find, owing to patchy and perhaps unpredictable distributions in time or space. Being unpredictable or "unapparent" (sensu Feeny 1976), these plants can potentially escape discovery by herbivores that specialize on them and may exhibit less costly defenses effective against the majority of other herbivores (qualitative defenses). Predictable resources with a high risk of discovery, such as mature leaves or late successional plants, are expected to have a large investment in broadly effective defenses (quantitative defenses). This theory suggests that the major selective force behind the evolution of plant defenses is a plant's apparency or its risk of discovery by herbivores.

Most of the information on plant/herbivore interactions comes from studies on the effectiveness of specific defenses from the viewpoint of the herbivore. These include surveys with generalists and investigations of more tightly coevolved systems between host and herbivore (Jones 1962, 1972, Ehrlich and Raven 1964, Gilbert 1971, 1975, Gilbert and Raven 1975, Jeremy 1976, Lawton 1976, Roeske et al. 1976, Edmunds

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and Alstad 1978). Another approach has been to document broad-scale associations of plant life history, successional status, habitat preference, or leaf age with either herbivory or plant defenses. Since these community level studies have examined patterns of herbivory and defense separately, their relationships can only be inferred (but see Rhoades, 1977*a, b*, McKey et al. 1978, Milton 1979, Oates et al. 1980). The general trend, however, is for higher concentrations and more effective defensive characteristics as well as lower grazing susceptibility in late successional or woody species, mature leaves, and plants of nutrient-poor areas (Kennedy and Booth 1951, Grime et al. 1968, Dixon 1970, Feeny 1970, 1975, 1976, Reichle et al. 1973, Dement and Mooney 1974, Janzen 1974, McKey 1974, 1979, Cates and Orians 1975, Johnson 1975, Lawton 1976, Rhoades and Cates 1976, Cates and Rhoades 1977, Hladik and Hladik 1977, Parker 1977, Rockwood and Glander 1977, Hamilton et al. 1978, Ives 1978, Levin and York 1978, McKey et al. 1978, Milton 1979, Bryant and Kuropat 1980, Coley 1980, 1981, 1982, Oates et al. 1980).

The goals of this study were to examine current theories of apparency and the evolution of plant defenses by simultaneously evaluating an array of plant characters and ecological factors. The following specific questions were posed for a range of plant species in a single community:

- 1) To what extent do plant species with different life histories vary in the levels of grazing damage?
- 2) Does leaf age affect patterns of herbivory?
- 3) What leaf characteristics are effective deterrents against herbivores, and how are they distributed within and between species?
- 4) Are temporal and spatial distributions of leaves and plants correlated with plant defenses and grazing damage?
- 5) Do investments in defenses and susceptibility to herbivores influence plant growth rates?

Rates of herbivory were measured under natural conditions, since it is the loss due to all available herbivores which is the important selective factor to the plant and not its palatability to a particular herbivore. Various physical, chemical, and nutritional characters of the leaf were measured and correlated with levels of herbivory and plant life histories. Although many plant properties deter herbivores, I chose to measure ones which were broadly effective, appeared to have dosage dependent effects, and could potentially be present in large concentrations.

STUDY SITE

The study was carried out in a lowland rain forest on Barro Colorado Island in Panama (9°10'N, 79°51'W). The completely forested 16-km² island has been protected as a biological reserve since 1923. The forest on approximately half of the island is estimated to be

at least 200 yr old (Foster and Brokaw 1982). Annual rainfall averages 265 cm (Rand and Rand 1979), the majority falling during a marked 8-mo wet season from late April to mid-December. Temperatures in the forest range from 22° to 28°C, and humidity from 80 to 90% (Rubinoff 1974). There is little seasonal variation. The vegetation is semideciduous and classified as tropical moist forest in the Holdridge Life Zone System (Holdridge and Budowski 1956, Holdridge et al. 1971). Recent detailed descriptions can be found in Knight (1975), Croat (1978), and Leigh et al. (1982).

METHODS

Study organisms

Patterns of herbivory and plant defenses were examined on Barro Colorado Island for 46 common tree species representing a range of plant families and growth forms. To examine effects of life history on herbivory and plant defenses, all species were classified into two life history groupings, pioneers or persistents, based on their ability to tolerate shade as saplings (Knight 1975, Whitmore 1975, 1978, Hartshorn 1978, 1980, Brokaw 1980, 1982, Denslow 1980). Persistent saplings grow throughout the forest understory. They can persist in this shaded condition for many years until a nearby tree falls, creating light and space in the canopy above. Pioneer saplings are only found in light gaps. They rely on rapid germination and establishment once a gap is formed. They grow much more rapidly, have less dense wood, and probably have shorter lifetimes than do persistent species. The two groups of species are equally important members of the forest, with pioneers making up ≈36% of the canopy tree species and 40% of the canopy individuals (Brokaw 1980).

Species were chosen for study based on their abundance both in the canopy and as juveniles in light gaps. Of the almost 200 tree species on Barro Colorado Island, many are extremely rare. For this study, 42 species of canopy trees were chosen from an initial list of 60 fairly common species (compiled with the help of R. Foster and N. Brokaw [*personal communication*]; Knight 1975, Croat 1978). Species were included for study if at least eight individual saplings between 1 and 2 m tall could be found growing in light gaps on the island. In addition to these 42 canopy species, four subcanopy tree species were included since data on grazing had been previously collected. They were *Croton bilbergianus*, *Desmopsis panamensis*, *Faramea occidentalis*, and *Swartzia simplex*. Twenty four of the 46 species are classified as persistents and 22 as pioneers. They represent 23 plant families, with pioneer and persistent species occurring together in 6 of them.

All work was done in light gaps made by fallen trees, because of their importance in forest regeneration and because the full complement of canopy species, both

pioneers and persistents, are found there (Jones 1945, Bray 1956, Steenis 1956, Schulz 1960, Aubreville 1971, Whitmore 1975, Hartshorn 1978, 1980, Veblen et al. 1979, Brokaw 1980). Saplings in gaps are also sufficiently small so that leaves could be reached and measured over time. Plants were studied in 49 gaps scattered over the island, chosen by size (100–500 m²) and apparent age (1–2 yr). The composition of each gap was determined by counting the number of individuals of each of the 46 study species. Gap areas were calculated by measuring the distance from a central point to the edge of the gap along eight compass points. Rough gap outlines were sketched on graph paper and areas quantified.

Herbivory

Grazing rates were monitored on 8600 marked young and mature leaves during the study. Approximately 10 1–2 m tall saplings in each species were tagged. An average of seven young and seven mature leaves on each sapling were arbitrarily chosen and marked for monitoring. Leaves were considered young from bud emergence until they had fully expanded and acquired adult coloring and toughness. Most young leaves were measured during an intermediate stage of expansion. Mature leaves sampled were older but not senescent. Leaves were marked with plastic-coated copper wires placed on the twig just below the leaf petiole. Direct observations of herbivores and measures of damage appeared similar on marked and unmarked leaves, suggesting that tags did not interfere with herbivore activity.

Rates of herbivory on these marked leaves were determined by measuring the total leaf area and the area of damage at time zero and 3 wk later. Areas were quantified by placing a clear plastic grid (62 squares/cm²) over the leaf and counting squares. Grazing rates were expressed as the percentage of the leaf area damaged per day, which corrects for absolute area changes in an expanding young leaf (Coley 1980). Grazing rates were monitored during three sample periods in 1979: dry season (26 February to 7 March), early wet season (24 May to 5 July), and late wet season (17 October to 22 November).

Rates of herbivory were obtained in 1979 for 20 pioneer and 21 persistent species. Data were not collected for *Ochroma pyramidale* or the four subcanopy trees, *Croton bilbergianus*, *Desmopsis panamensis*, *Fareaea occidentalis*, and *Swartzia simplex*. Measures of herbivory on these species are from 1977 (Coley 1980), but since sample period lengths were slightly different, they are deleted from several analyses. Statistical comparisons involving patterns of herbivory are therefore performed on just 41 species.

The types of leaf damage considered for the estimation of grazing rates were holes, mines, galls, and scraped leaf surfaces caused by herbivorous insects. In addition, I included necrotic areas, which may be

due to microbial or fungal infection or to tissue death resulting directly from grazing. Although some feeding by mammals was observed, it was extremely rare in gaps and was excluded from the analysis. Leigh and Smythe (1978) estimate that 85% of the leaf loss in the canopy on Barro Colorado Island is due to insects. Since the major selective force on the evolution of plant defenses in this forest community is assumed to be from insects and perhaps microbes, I focused on these types of damage.

To determine the effects of density and clumping on grazing damage experimentally, three species were planted at two different densities in natural light gaps. One pioneer species, *Miconia argentea*, and two persistent species, *Trichilia cipo* and *Prioria copaifera*, were used. These species are typical of the two life history categories, with respect to levels of defensive characteristics and rates of growth and herbivory. Seeds of each species were collected from one parent to minimize genetic differences and grown under herbivory-free conditions in a greenhouse for 1–1.5 yr prior to transplanting. Individuals were paired by height and number of leaves and were assigned randomly to one of the two density treatments. For the high-density treatment, individuals were added to light gaps with the highest naturally occurring densities of conspecifics. For the low-density treatment, individuals were planted in gaps with no other conspecifics. These conditions were chosen to maximize the probability of observing differences in herbivory due to spatial distributions of individuals. Plants were transplanted in the 1st wk of June 1980 and measured for grazing damage 6 wk later.

Growth rates

Height of marked plants was measured every 3 mo from December 1978 until December 1979 to determine annual growth rates. All plants were between 0.5 and 1.5 m tall at the beginning of the study. The measure of height growth, which was most independent of original size, was the absolute height increment. The number of young and mature leaves present in a plant was noted in December 1978 and March, May, July, and October 1979. The total number of leaves produced during the year was also counted.

Plant antiherbivore mechanisms

Various physical, chemical, and nutritional properties of leaves that have been shown to affect levels of grazing were measured directly in the field and on field-collected samples in the laboratory. Though there are numerous plant characters which deter herbivores, I chose to measure quantifiable ones that probably represent the major defensive costs to the plant. I measured the concentrations of simple and condensed phenolic compounds, various components of fiber, leaf toughness, pubescence, and water and nitrogen content for young and mature leaves. Concentrations of

phenolic compounds were measured using three colorimetric assays modified from those used by D. Rhoades (*personal communication*). The Folin Denis method quantifies total phenolics including simple phenols or hydrolyzable tannins, but it is somewhat influenced by the degree of polymerization (Swain and Goldstein 1964) and may also react with nonphenolic compounds. Values were standardized against tannic acid (Sigma, lot No. 64C-0093). Leucoanthocyanin and Vanillin methods were used to determine concentrations of condensed tannins and related flavonoids. These long-chain polyphenols are presumed to be more efficient binders with protein (Swain 1965, 1979). The Leucoanthocyanin method measures leucoanthocyanin-based phenols, with quebracho tannin as a standard (Harshaw Chemicals, Glasgow, Scotland, Lot No. 65). Catechin (Sigma, Lot No. 66C-0185) and epicatechin (Sigma, Lot No. 46C-0021) were used as the standard for the Vanillin method, which is sensitive to free catechin and catechin-based condensed tannins. The actual concentrations of phenolic compounds in the leaves are estimated in terms of equivalent concentrations of the above standards, although the identity of leaf phenolics also affects values.

Leaf samples for phenol analysis were collected from saplings in conditions comparable to plants being measured for grazing damage. Undamaged leaves from 5 to 15 plants of each species were collected and pooled due to time restrictions. This assured a more accurate mean measure of phenolic content for each species, but masked between-individual variation. Young and mature leaves were treated separately. For all analyses, young leaves were sampled when they were approximately half expanded. Twigs containing several leaves were cut, placed in plastic bags, and immediately put in an ice chest to keep them cold but not frozen. Samples were in this condition for not >4 h prior to extraction. Leaf areas and fresh masses were taken on all samples. A portion of the sample was processed for phenols, and the remainder dried at 65°C to obtain dry masses and water content and for analysis of fiber and nitrogen (see below). For phenolic assays, 2 g fresh mass of leaves were homogenized in 35 mL of 85% methanol, brought to 50 mL, boiled for 20 min, cooled, filtered, and stored in the refrigerator for up to a week. Samples prepared in this fashion remain stable for at least 3 wk. All phenolic assays were done on this methanol extract. Samples were collected once during the dry season (20 March to 3 April 1979) and once in the wet season (13–31 August 1979).

The dried portion of the leaf samples collected for phenolic assays in the wet season was also used to determine fiber content. Fiber analyses were performed according to the detergent method of Van Soest (Goering and Van Soest 1970) by the University of Alaska Palmer Agricultural Station. Neutral-detergent fiber (NDF) includes all cell wall constituents. NDF is

essentially indigestible except through microbial fermentation and is separated from the soluble and nutritionally available cell material by this procedure. The acid-detergent fiber (ADF) procedure determines lignocellulose content and is preparatory for lignin and insoluble ash determination and, by subtraction, cellulose content.

The percentage of total nitrogen was determined by micro-Kjeldahl digestion at the University of Alaska Palmer Agricultural Station on dried, ground leaf tissue. Samples for wet-season estimates were the same as those collected for fiber and phenolic analysis. In addition, a dry-season sample collected in January 1979 was analyzed.

Leaf toughness was measured on freshly collected leaves, using a punchmeter modeled after a design by Feeny (1970). It measures the force necessary to punch a rod 5 mm in diameter through the leaf. This gives an index of toughness, in newtons.

Statistical analyses

A log transformation of the grazing rates (percent leaf area damaged per day) was performed to equalize variances. Because grazing means were proportional to their standard deviations and because grazing percentages were zero or small, the following log transformation was justified (Snedecor and Cochran 1967, Bliss 1970): $\ln(1000 \times \text{grazing rate} + 1)$. The significance of differences in means between pioneers and persistents was determined by a nested, crossed analysis of variance on the log-transformed grazing rates. Since the wet season on Barro Colorado Island lasts for two-thirds of a year, annual rates of herbivory for each species are the average of the two wet-season and one dry-season samples (using leaves as replicates).

Differences in the distribution of grazing damage among leaves and among plants was evaluated using several statistical methods. The variation in grazing damage among leaves within a plant (Table 8: between-leaf variance) was compared for pioneer and persistents by a nested ANOVA on the $\ln(100 \times s^2_{ijk} + 1)$, where s^2_{ijk} is the plant variance of the log-transformed grazing rate on leaves (Bliss 1970). Analyses were done on unweighted within-cell variances as well as on values weighted by the number of leaves per plant.

To evaluate the time scales over which variation in grazing damage occurs, analyses were done by seasons and for the year as a whole. Values for the seasonal estimate of within-plant variance in grazing (Tables 6 and 8: seasonal) were calculated separately for each 3-wk sampling period, (1) dry, (2) early wet, and (3) late wet seasons, and then averaged. Seasonal estimates, therefore, indicate the average within-season variance in damage for a given plant. Longer-term variation in grazing (Tables 6 and 8: annual) was determined by pooling all leaves for each plant, without

regard for season, to give an annual estimate of variance.

The between-plant variance in grazing damage (Tables 6 and 8) was expressed as the percentage of the total variance for a species that was attributed to between-plant differences only. This was calculated as the intraclass correlation: $[100 \times (\text{variance component for plants}/\text{total variance})]$, derived from an ANOVA on the log-transformed grazing rates. As with between-leaf variance measures, between-plant variances were determined for the three seasons separately (seasonal) and for the year combined (annual).

A final measure of dispersion used to compare grazing damage among plants is referred to as between-plant skewness (Tables 6 and 8). This value is the skewness for a species in the average untransformed grazing rate on each plant. As with the other variance measures, it was calculated for the seasons separately and pooled.

The degree of synchrony in leaf emergence patterns was calculated as the coefficient of variation for the number of young leaves present on a plant at each of six sample times throughout the year. A high value indicates a close degree of synchrony and a low value a more even production of young leaves over the year.

Discriminant function and factor analyses (SAS statistical packages) were used to compare the similarity of pioneer and persistent species based on leaf characters (Cooley and Lohnes 1971, Sneath and Sokal 1973). The discriminant function determines the best linear combination of leaf variables that classify species into designated groupings, in this case the two life histories. The factor analysis used employs a varimax rotation technique and maximizes the separation of species independent of life history. For factor analysis, variables were standardized with a z -transformation to eliminate effects of the unit of measure.

RESULTS

Herbivory

There are large differences in rates of herbivory among leaf age-classes and among life history groups. Annual rates of herbivory are higher on young than on mature leaves for all 24 persistent species and for 14 of the 22 pioneer species (see Appendix). For both groups, young leaves are grazed more rapidly than mature leaves, regardless of season, 3 times faster for pioneers and almost 25 times faster for persistents ($P < .001$, ANOVA, Table 1). An examination of life histories shows pioneer species to be indistinguishable from persistents when compared for grazing damage on young leaves ($P > .2$, ANOVA). The mature leaves of pioneers, however, are eaten six times more rapidly than those of persistents ($P < .001$, ANOVA). These trends are consistent for all seasons. Although overall levels of herbivory are slightly lower in the dry season than in either the early or late wet season, these dif-

TABLE 1. Rates of herbivory on young and mature leaves of 20 pioneer and 21 persistent species. Values followed by different superscript letters are significantly different ($P < .001$). Significance levels were determined by a two-way nested ANOVA on the log-transformed grazing rate, considering leaves as replicates (see text).

	Pioneer species			Persistent species		
	% grazed/d	No. plants	No. leaves	% grazed/d	No. plants	No. leaves
Annual average*						
Young	0.83 ^a	202	1618	0.97 ^a	232	2369
Mature	0.24 ^b	202	1807	0.04 ^c	198	2874
Dry season†						
Young	0.46 ^a	83	232	0.73 ^a	85	489
Mature	0.13 ^b	117	455	0.03 ^c	134	773
Wet season‡						
Young	0.89 ^a	190	1386	1.03 ^a	213	1880
Mature	0.28 ^b	180	1352	0.05 ^c	193	2101

* Average of three sample periods based on an 8-mo wet season and a 4-mo dry season.

† Rates determined during February and March 1979.

‡ Average of rates for early wet season, May and June 1979, and late wet season, October and November 1979.

ferences are not significant ($P > .05$, t test). Annual rates of grazing will therefore be used to estimate susceptibility to herbivory throughout the remainder of this paper.

The variation in annual rates of herbivory among leaf age-classes and different species spans four orders of magnitude (Appendix, Fig. 1). Young leaves of *Tabebuia rosea* are grazed most heavily, 2.8%/d, as compared with mature leaves of two persistent species, *Calophyllum longifolium* and *Aspidosperma megalocarpon*, which are grazed $<0.0003\%/d$. The frequency distributions of the average annual grazing rates on young leaves of pioneer and persistent species are very similar (Fig. 1). The range of grazing rates on mature leaves of persistent species, however, is smaller and significantly lower than that of the other three leaf groups (Fig. 1, $P < .01$, Mann-Whitney U).

In this study there do not appear to be phylogenetic constraints on defenses as indicated by their effectiveness in reducing herbivory. In all six families having both pioneer and persistent members, the pioneers are grazed more than the persistents. In the Annonaceae, Bombacaceae, and Moraceae, and for two *Zanthoxylum* species in the Rutaceae, there are one to two orders of magnitude difference in damage levels between pioneer and persistent species. This is comparable to that found between pioneers and persistents in general. For the Burseraceae and two *Cupania* species in the Sapotaceae, the difference between pioneer and persistent members is in the same direction but not as great. Grazing susceptibility therefore seems more closely correlated with plant life history than with phylogenetic relatedness.

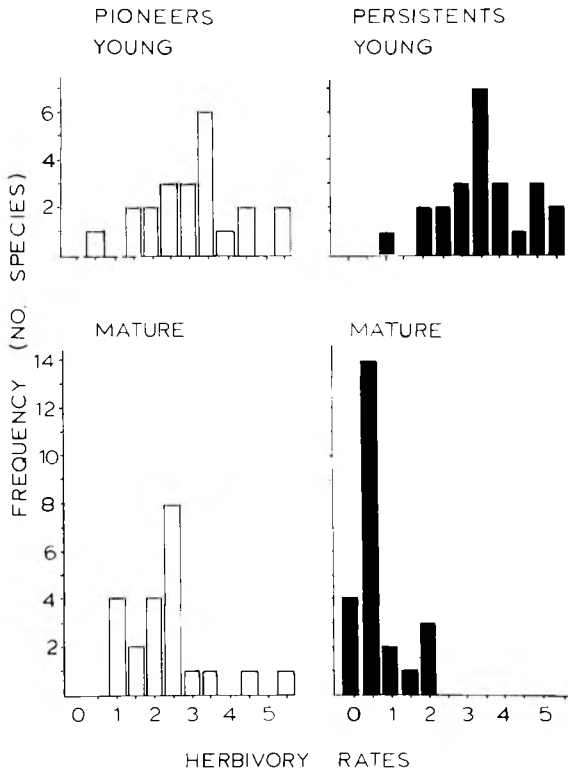


FIG. 1. Frequency distributions of rates of herbivory on young and mature leaves of 22 pioneer and 24 persistent species. Grazing rates are expressed as: $\ln[(1000 \times \% \text{ leaf area damaged/day}) + 1]$. The distribution of mature leaves of persistents is significantly different from all others ($P < .001$, Mann-Whitney U).

Defensive characteristics of leaves

I measured various chemical, physical, and nutritional properties of leaves to determine which characters might be responsible for the large differences in grazing rate and to identify a relationship between the level of defense and plant life history or leaf age. Differences between the two life history categories in the defensive mechanisms of mature leaves parallel differences in their susceptibility to herbivory (Table 2). The mature leaves of pioneers, which are grazed more heavily than those of persistents, have lower levels of both simple and condensed phenolics. Concentrations are 3 times less (0.8 vs. 2.7%, and 1.7 vs. 4.8% dry mass; $P < .05$, Mann-Whitney U) for the condensed tannins. Mature pioneer leaves are also significantly less fibrous as measured by Neutral- and Acid-Detergent fiber, lignin, and cellulose contents, and are only two-thirds as tough as persistent leaves. Pubescence is the only measured defense better represented in pioneers. Sixty-five percent of the pioneer species are pubescent as compared to only 25% of the persistent species ($P < .05$, chi-square). The average densities of hairs on the upper and lower leaf surfaces are also significantly higher for pioneers. Nutritional quality of

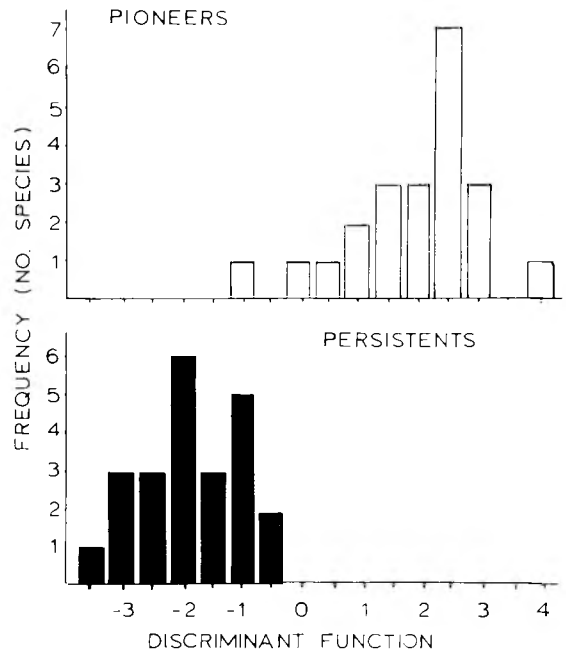


FIG. 2. Plot of species frequencies for 22 pioneer and 24 persistent species classified by a discriminant function analysis based on defenses of mature leaves (see Table 3).

mature pioneer leaves is better than that of persistents, due to a slightly higher nitrogen concentration (2.5 vs. 2.2% dry mass) and a substantially higher water content (70 vs. 62%; $P < .05$, Mann-Whitney U).

Although the mean values for various defenses differ significantly between pioneer and persistent species, the range within a life history can be large and the overlap between groups substantial. Defenses of mature leaves of pioneer species have higher coefficients of variation than those of persistent species for all 16 of the measured defenses except cellulose and nitrogen. Not all persistents are well defended by all types of defenses. *Aspidosperma megalocarpon*, *Quararëbea asterolepis*, and *Poulsenia armata*, three shade-tolerant persistents, have very low levels of condensed tannins in the mature leaves, yet all are extremely tough. Similarly, there are pioneer species such as *Cassearea arborea*, whose mature leaves have a high fiber content (NDF), and *Hyeronima laxiflora*, which has high levels of condensed tannins. Despite individual exceptions such as these, there are significant correlations between several defenses. For leaves in general, toughness is positively correlated with fiber measures ($P < .05$), and both are negatively correlated with nutritional content ($P < .05$). Phenolic measures are correlated with each other ($P < .05$) but not with any other leaf characters. Pubescence is negatively related to toughness ($P < .05$). Although these defenses are significantly correlated, the coefficients are not large (in general, $r < .4$).

TABLE 2. Defensive characteristics of young and mature leaves of pioneer and persistent canopy tree species. Values within a row followed by different superscript letters are significantly different ($P < .05$, Mann-Whitney U).

	Pioneer (22 species)				Persistent (24 species)			
	Young		Mature		Young		Mature	
	Mean	Range	Mean	Range	Mean	Range	Mean	Range
Chemical								
Total phenols (% dry mass)	12.7 ^b	2.9–37.8	7.7 ^a	2.6–19.1	19.2 ^c	1.7–38.9	10.1 ^a	1.7–22.6
Tannins—Vanil (% dry mass)	1.7 ^a	0.04–8.4	0.8 ^a	0.03–3.4	5.1 ^c	0.03–15.8	2.7 ^b	0.04–7.8
Tannins—Leuco (% dry mass)	3.4 ^a	0–25.2	1.7 ^a	0–7.5	9.7 ^c	0.5–24.6	4.8 ^b	0.07–13.2
Fiber—NDF (% dry mass)	38.1 ^a	13.7–62.5	43.6 ^a	27.2–64.2	40.4 ^a	17.5–61.8	51.3 ^b	32.8–67.5
Fiber—ADF (% dry mass)	27.5 ^a	9.3–43.3	29.5 ^a	19.7–47.7	31.5 ^a	7.4–55.8	37.4 ^b	15.6–49.9
Lignin (% dry mass)	9.6	0.9–17.7	10.5	3.3–18.5	11.7	1.4–21.5	12.5	3.3–20.8
Cellulose (% dry mass)	17.0 ^a	7.4–30.4	17.6 ^a	10.2–30.4	19.5 ^a	5.9–41.6	23.4 ^b	12.2–30.3
Physical								
Toughness (N)	2.20 ^a	1.24–4.53	3.84 ^b	2.46–7.09	2.45 ^a	1.54–4.75	6.10 ^c	2.73–11.56
Hairs (% of species)	65 ^b		65 ^b		38 ^a		25 ^a	
Hairs—upper (no./mm ²)	1.9 ^c	0–7.0	0.4 ^b	0–1.8	0.5 ^b	0–6.7	0 ^a	0–0
Hairs—lower (no./mm ²)	6.2 ^b	0–18.0	5.1 ^b	0–18.0	1.4 ^a	0–10.0	0.5 ^b	0–3.4
Nutritional								
Water (%)	74 ^c	63–83	70 ^b	57–82	76 ^c	66–88	62 ^a	49–77
Nitrogen (% dry mass)	3.2 ^b	2.1–4.3	2.5 ^a	1.7–3.1	3.3 ^b	1.8–5.1	2.2 ^a	1.2–3.1

Differences between pioneers and persistents in defenses for young leaves are not as dramatic as for mature leaves (Table 2). Frequency distributions of defenses show almost complete overlap. Young leaves of pioneer and persistent species are grazed to the same extent, have similar concentrations of fiber, water, and nitrogen, and are equally tough. Young persistent leaves, however, do have significantly lower hair densities and two to three times the phenolic concentrations.

In general, young leaves of pioneer and persistent species are fairly similar, with the major differences existing between young and mature leaves regardless of life history (Table 2). As a class, young leaves are approximately half as tough, less fibrous by all measures, and significantly more nutritious than mature leaves. They are also more densely pubescent, often completely losing their hairs once fully expanded. The concentrations of both simple and condensed phenolics, however, are substantially higher in the young leaves. The concentration of total phenols is 39% dry mass in young leaves of *Simarouba amara* and levels of condensed tannins reach 15–25% (dry mass) in *Macrocneum glabrescens* and *Prioria copaifera* (see Appendix).

Multivariate analyses.—A discriminant function analysis was used to determine if pioneer and persistent species could be separated accurately by differences in their defenses. Based on the defenses of mature leaves, the discriminant function correctly classifies 96% of the species, or 44 of the 46 for which complete information is available (Canonical correlation = .89, chi-square of Wilk's lambda = 56.3, 15 df, $P < .0001$). In general, species can be clearly separated into life history groupings based on defenses of mature leaves, and the marginal species in the discrim-

ination are also the species with intermediate shade tolerance (Fig. 2). The two species which were misclassified as persistents were *Cupania fulvida* and *Casearea arborea*. *C. fulvida* is one of the most shade-tolerant pioneer species (Knight 1975, Brokaw 1980), and all its defenses are similar to the mean values for persistent species. *C. arborea* is clearly dependent on light gaps. Although it is typical of pioneers in having low phenols and toughness and high water and nitrogen contents, it has the second highest NDF content (64%, see Appendix) of all species. The persistent *Simarouba amara* was classified correctly but falls near the division between pioneers and persistents. It is a fast-growing species and probably fairly light dependent. Based on shade tolerance, we would expect *Zanthoxylum panamense* and *Tabebuia rosea* also to be marginally classified. However, *Z. panamense*, a persistent, is placed near the center of the persistent grouping (discriminant score = -2.4, Fig. 2), and the pioneer *Tabebuia rosea*, although very shade tolerant (Brokaw 1980, P. D. Coley, *personal observation*), lies well within the pioneer grouping (discriminant score = 2.1, Fig. 2).

The relative importance of each defensive characteristic in classifying pioneer and persistent species was determined for the discriminant analysis. Because the discriminant function takes correlations between variables into account in the standardized coefficients, a correlation of each defense with the discriminant function indicates the contribution of each defense to the separation (Table 3). Toughness and water content of mature leaves are most highly correlated with the discriminant function, followed by various fiber measures, nitrogen, and finally phenolic contents. As was suggested by mean defense values in Table 2, pioneers are less tough, have lower concentrations of phenols

TABLE 3. Discriminant function analysis for the classification of 22 pioneer and 24 persistent species based on defenses of mature leaves. Defenses are ordered by the correlation with the discriminant function.

	Standardized discriminant function coefficient	Correlation with discriminant function
Toughness	-1.36	-.35
Water	-0.82	.34
Cellulose	1.24	.31
Hairs—upper	0.56	.28
Fiber—ADF	2.53	-.28
Hairs—lower	0.46	.25
Fiber—NDF	-1.54	-.21
Tannins—Leuco: protein	*	-.19
Tannins—Leuco	-2.12	-.16
Tannins—Vanil: protein	0.31	-.14
Nitrogen	0.13	.14
Tannins—Vanil	0.98	-.13
Total phenols: protein	1.29	-.12
Lignin	-2.89	-.11
Lignin: ADF	2.79	.10
Total phenols	-1.07	-.08

* Failed tolerance test.

and fiber, and have higher concentrations of nitrogen and water. They are also more pubescent.

A discriminant analysis is unable to separate pioneer and persistent species using only defensive characters of young leaves. The function was not significant for young leaves (canonical correlation = .67, chi square of Wilk's lambda = 21.6, 16 df, $P = .16$) and only classified 35 of the 46 species correctly (76%).

Factor analysis was also used to examine the similarity of species with respect to their defensive characteristics (Cooley and Lohnes 1971). Unlike the discriminant function analysis, factor analysis determines the axes (factors) without regard to the classification groups of interest. A factor analysis was performed on the defensive properties of mature leaves, standardized (mean = 0, standard deviation = 1) to remove effects of units of measure. The factor score coefficient of each defense is given for factor I and factor II, which together explain 52% of the variance (Table 4). Pioneer and persistent species are separated into two fairly distinct but dispersed groups with the first two factors (Fig. 3). Although species are divided by life history, they do not cluster by family, and related pioneer and persistent species can be far apart. Furthermore, the three understory trees *Faramea occidentalis*, *Desmopsis panamensis*, and *Swartzia simplex*, which are all in different families, group together near 0,0. It seems, therefore, that habitat and life history place greater constraints on these major defenses than do phylogenetic relationships.

Many of the same species that were marginally classified by the discriminant function are also outliers using factor analysis. *Casearea arborea* and *Cupania fulvida*, misclassified by discriminant analysis, lie outside the general range occupied by pioneers plotted

TABLE 4. Factor analysis based on defenses of mature leaves for 22 pioneer and 24 persistent species. Eigenvalues, percent variance explained, and scores are given for factors I and II.

	Factor I	Factor II
Eigenvalue	13.4	10.5
% variance	29.1	22.9
Defenses	Factor scores	
Hairs—upper	+2.69	-1.65
Lignin: ADF	+1.07	+0.36
Tannins—Leuco	-0.96	-0.14
Hairs—lower	+0.94	-0.60
Tannins—Vanil	-0.93	-0.24
Tannins—Leuco: protein	-0.88	-0.49
Tannins—Vanil: protein	-0.86	-0.49
Nitrogen	+0.86	+1.65
Fiber—NDF	+0.64	+1.93
Toughness	-0.56	-0.75
Water	-0.54	-0.03
Fiber—ADF	-0.45	+0.93
Cellulose	-0.40	+0.56
Total phenols	-0.39	+0.76
Total phenols: protein	-0.38	-1.20
Lignin	+0.16	+0.98

with factors I and II (Fig. 3). The two other extremes in the factor analysis, *Tabebuia rosea* and *Zanthoxylum panamense*, were not misclassified by the discriminant function but show intermediate shade tolerance. *Simarouba amara* and *Alseis blackiana* are both fast-growing species, probably less shade tolerant than most persistents, and occur at the pioneer/persistent interface (Fig. 3). The pioneer *Ochroma pyramidale* is placed within the persistents because of fairly high concentrations of phenols. This association is unclear based on life history characters since *Ochroma* is one of the most light-dependent and fast-growing pioneer species.

Defenses and herbivory

For mature leaves, differences between species in defensive characteristics explain 70–80% of the variance in grazing damage among species. This was determined by a stepwise multiple regression of the log-transformed grazing rates against the 16 measured defensive characteristics of leaves. For pioneer species $r^2 = .86$, $P = .04$; for persistent species $r^2 = .74$, $P = .03$, and for all species combined $r^2 = .70$, $P < .001$. All variables improve the r^2 estimate, but only a few make statistically significant contributions. For persistent species and all species pooled, toughness and water content are among the most important predictors. For pioneers, a combination of nitrogen and lignin, a component of fiber, gives a better estimate. Since there are correlations between fiber and toughness and between nitrogen and water, the general pattern for mature leaves is that fiber and nutritional measures together are the best predictors. Hair density is also a good predictor of grazing damage, but the positive cor-

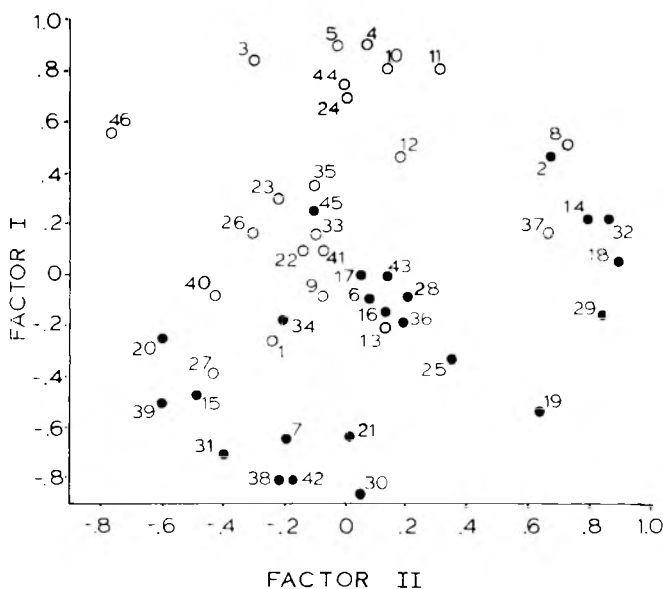


FIG. 3. Plot of 22 pioneer and 24 persistent species in relation to Factors I and II from a factor analysis based on defenses of mature laves (see Table 4). Pioneers are represented by ○ and persistents by ●. Species identification numbers are listed below:

1 <i>Alchornea costaricensis</i>	13 <i>Cupania fulvida</i>	24 <i>Luehea seemannii</i>	35 <i>Spondias radlköferi</i>
2 <i>Alseis blackiana</i>	14 <i>Cupania sylvatica</i>	25 <i>Macrocnemum</i>	36 <i>Swartzia simplex</i>
3 <i>Annona spraguei</i>	15 <i>Cyanodendron</i>	26 <i>Miconia argentea</i>	37 <i>Tabebuia rosea</i>
4 <i>Apeiba membranacea</i>	16 <i>Desmopsis panamensis</i>	27 <i>Ochroma pyramidale</i>	38 <i>Tachigalia versicolor</i>
5 <i>Apeiba tibourbou</i>	17 <i>Faramea occidentalis</i>	28 <i>Poulsenia armata</i>	39 <i>Tetragastris panamensis</i>
6 <i>Aspidosperma megalocarpon</i>	18 <i>Guarea glabra</i>	29 <i>Pouteria unilocularis</i>	40 <i>Trattinickia aspera</i>
7 <i>Calophyllum longifolium</i>	19 <i>Guarea multiflora</i>	30 <i>Prioria copaifera</i>	41 <i>Trema micrantha</i>
8 <i>Casearea arborea</i>	20 <i>Guatteria dumetorum</i>	31 <i>Protium tenuifolium</i>	42 <i>Trichilia cipo</i>
9 <i>Cecropia insignis</i>	21 <i>Hirtella triandra</i>	32 <i>Quararebea asterolepis</i>	43 <i>Virola sebifera</i>
10 <i>Cecropia obtusifolia</i>	22 <i>Hyeronima laxiflora</i>	33 <i>Sapium caudatum</i>	44 <i>Zanthoxylum belizense</i>
11 <i>Cordia alliodora</i>	23 <i>Jacaranda copaifera</i>	34 <i>Simarouba amara</i>	45 <i>Zanthoxylum panamense</i>
12 <i>Croton bilbergianus</i>			46 <i>Zuelania guionia</i>

relation suggests it is indicative of poorly defended species.

Although these leaf characters account for most of the variation among species in grazing on mature leaves, they explain very little for young leaves. None of the single or multivariable regressions of grazing on defenses are significant. For young leaves of pioneers and persistents combined, only 30% of the variation in grazing damage is explained using all leaf defenses. As with mature leaves, various fiber measures and pubescence are the best predictors, although they are not significant. Nutritional measures, which are important predictors of damage for mature leaves, are not so for young leaves. Since concentrations of protein and nitrogen are higher in young leaves, the levels may not be limiting to herbivores. These results therefore suggest that young leaves are not depending on the same defensive mechanisms as mature leaves.

A multiple regression identifies the group of defenses which together best predicts rates of herbivory. However, if two defenses are highly correlated, only one will be heavily weighted in the regression equa-

tion. An alternative measure of the effectiveness of individual defenses is therefore the correlation of that characteristic with herbivory. For mature leaves of both pioneers and persistents, leaf toughness is the variable with the highest negative correlation with herbivory ($r = -.515$, $P < .01$, Table 5). All measures of fiber content are also negatively correlated with grazing, but lignin is the least so. For mature persistent leaves, nutritional quality appears to be an important correlate of grazing damage. Phenols, when considered as straight concentrations or as a ratio with nitrogen, are the only class of defenses that is not significantly related to rates of herbivory. Pubescence is very highly correlated with grazing, but the relationship is positive. This is clearly not due to a direct positive effect of hairs on herbivory, but is probably because hairs are negatively correlated with more-effective defenses.

For young leaves, none of the 16 defensive characters is significantly correlated with grazing damage, except for leaf toughness in persistent species ($r = .473$, $P < .05$, Table 5). By chance alone one would

TABLE 5. Correlation coefficients between rates of herbivory and defenses of young and mature leaves. Values are based on 22 pioneer and 24 persistent species using the log-transformed grazing rate.

	Young leaves			Mature leaves		
	Pioneer	Persistent	Both	Pioneer	Persistent	Both
Chemical						
Total phenols (% dry mass)	.014	.030	.040	-.145	.109	-.099
Tannins—Vanil (% dry mass)	.278	.182	.190	-.130	.023	-.112
Tannins—Leuco (% dry mass)	.220	.207	.209	-.087	.220	-.128
Fiber—NDF (% dry mass)	.229	.180	.254	-.119	.056	-.278*
Fiber—ADF (% dry mass)	.302	.095	.181	-.318	-.056	-.424*
Lignin (% dry mass)	.213	.148	.133	-.219	.101	-.223
Cellulose (% dry mass)	.340	.036	.195	-.348	-.147	-.473**
Physical						
Toughness (N)	.011	-.473*	-.045	-.360	-.363	-.515**
Hairs—upper (no./mm ²)	.001	-.219	-.146	-.040	.000†	.291**
Hairs—lower (no./mm ²)	.062	-.306	-.114	.591**	.089	.635**
Nutritional						
Water (%)	.156	-.082	.081	-.027	.448*	.507**
Nitrogen (% dry mass)	.028	-.237	.004	.010	.278	.287*
Tannin: protein ratios						
Total phenols: protein	-.031	.124	.093	-.125	.037	-.183
Tannin—Vanil: protein	.289	.111	.167	-.161	.049	-.161
Tannin—Leuco: protein	.292	.133	.191	-.182	.145	-.184

* $P < .05$, one-tailed; ** $P < .01$, one-tailed.

† None of these species is pubescent on the upper surface.

expect two significant correlations ($.05 \times 45$ comparisons); however, since toughness was negatively correlated with grazing on mature leaves, it may also be important in young leaves. Fiber and tannin contents of young leaves show a weak but positive relationship to grazing, even for partial correlations which exclude effects of other defenses. This is the reverse of what was expected for young leaves and observed for mature leaves.

Spatial distribution and herbivory

Field tests.—Since the theory of plant apparency suggests that poorly defended plants rely on escape from their specialist herbivores (Feeny 1976, Rhoades and Cates 1976), spatial distributions of plants in gaps were quantified to see if they differed between life histories and if this was reflected in decreased herbivory. Despite dramatic differences in life histories and dependency on light gaps, there is no difference in the distribution of pioneer or persistents among gaps (Table 6). The average abundances of the two groups are identical ($P > .5$, Mann-Whitney U , Table 6). They also do not differ in the degree of clumping, as measured either by Lloyd's (1967) patchiness index, or by the average variance for each species in the number of individuals per gap.

A more direct measure of whether individual plants are avoiding discovery by herbivores can be made by examining the distribution of grazing damage among plants of a single species. If some individuals are escaping and suffering little damage and others are found and eaten, then one would expect a high variance in

grazing among plants within a species. The percent of the total variation in damage for a species which is due to the between-plant component (intra-class correlation) is significantly greater for pioneer than for persistent species when analyzed within each season's 3-wk sample period (Table 6: seasonal). There are no differences between the seasons in the between-plant variance. The pattern is somewhat diminished, but still significant, when the seasons are pooled and one considers grazing damage per plant throughout the year (Table 6: annual).

Another measure for dispersion of damage which may reflect discovery patterns of herbivores is the skewness for a species in the damage to individual plants. Both pioneer and persistent species are positively skewed ($P < .05$, Table 6), meaning more individuals have damage rates below the mean than in a normally distributed population. Skewness both within seasons and over the entire year is greater for persistent species, indicating that a larger fraction of each population has reduced levels of damage.

The effects of spatial distributions on herbivory were further explored by determining the correlation between grazing damage on individual plants and the density and identity of neighbors in the same gap. Theories of plant apparency predict that isolated individuals of poorly defended species should show lower damage rates than clumped individuals (Feeny 1976, Rhoades and Cates 1976). For each of the 42 study species, grazing damage per plant was regressed against various measures of spatial distribution, expressed as the numbers and densities of individuals and species

TABLE 6. Spatial distribution of plants and dispersion in rates of herbivory on mature leaves. Significance of comparisons within rows determined by a Mann-Whitney *U* test.

	Pioneers (<i>n</i> = 20)	Persistents (<i>n</i> = 21)
Plant distribution		
No. individuals/100 m ² †	0.40	0.40
No. individuals/gap†	1.05	1.04
Variance/gap‡	11.3	9.9
Patchiness§	8.77	7.85
Rates of herbivory		
Between-plant variance		
Seasonal¶	30.0	13.4*
Annual¶	15.5	8.2*
Between-plant skewness		
Seasonal¶	1.72	1.91
Annual¶	1.89	2.35*

* *P* < .05.

† Mean density per species; *n* = 59 gaps.

‡ Average variance in the number of individuals per gap for each species.

§ Lloyd's (1967) patchiness index.

¶ Analyses done by season and then averaged, indicating mean dispersion values for grazing in a 3-wk period.

¶ Analyses done with seasons pooled, indicating mean dispersion values over the entire year.

in each gap. Only 3% of the regressions were significant (*P* < .05). The frequency of negative signs for the regression slopes was compared for pioneers and persistents (chi-square one-sample test). Grazing was examined as a function of the abundance of conspecifics, pioneers, persistents, and of all species combined. Gap area and the abundance of conspecifics have no effect on grazing for any leaf group. For persistent species, none of the measures of gap composition affects grazing rates on young or mature leaves. Fifteen of the 20 pioneer species showed a negative relationship between grazing on mature leaves and the abundance of either pioneer or persistent individuals in the gap. This pattern is the reverse of what is predicted if plants are avoiding damage through spatial escape.

Experimental test.—An experimental test of the effects of spatial clumping on levels of herbivory was conducted by planting individuals of two persistent species, *Prioria copaifera* and *Trichilia cipo*, and one pioneer species, *Miconia argentea*, in different densities in the field and monitoring rates of herbivory. Grazing damage was measured 1.5 mo after transplanting, so it includes herbivory on leaves during both young and mature phases. It was predicted that if escape is occurring, it should be seen as a reduction in grazing damage primarily for the poorly defended pioneer *Miconia argentea*. The better-defended persistent species are not expected to show strong density-dependent effects. Although the experiment was designed to maximize the probability of observing evidence of escape, there is no significant effect (*P* > .2) of density on grazing for any species (Table 7).

TABLE 7. Effects of density on rates of herbivory (% of leaf area lost per day) for experimental plantings of individuals in naturally occurring light gaps. A paired *t* test was used to compare individuals from high- and low-density treatments.

	No. pairs	Mean grazing (%/d)		<i>P</i>
		High density	Low density	
Pioneer				
<i>Miconia argentea</i>	14	1.25	0.95	> .2
Persistents				
<i>Prioria copaifera</i>	25	0.009	0.006	> .5
<i>Trichilia cipo</i>	15	0.010	0.038	> .4

Temporal distribution and herbivory

The temporal availability of young leaves has been suggested as a means of satiating or escaping from herbivores (McKey 1974, Feeny 1976, Rhoades and Cates 1976). This was examined by quantifying the temporal patterns of leaf emergence for individual plants throughout the year. Representatives of two distinct leaf emergence patterns are presented in Fig. 4. *Tachigalia versicolor* typifies a pattern common in persistents where there are one or two periods of leaf emergence synchronized within and between individuals. All young leaves on the plant are therefore at the same stage of expansion. The pattern seen for *Cecropia insignis* is characteristic of pioneer species, which tend to have a steady production of young leaves throughout the year. The degree of synchrony in leaf emergence for an individual plant was quantified by a

TABLE 8. Temporal distribution and dispersion in rates of herbivory on young leaves. Temporal measures were tested by a Mann-Whitney *U*. None of the grazing measures was significantly different. See Table 6 for an explanation of categories.

	Pioneers (<i>n</i> = 20)	Persistents (<i>n</i> = 21)
Temporal distribution		
Leafing synchrony (cv)	0.64	1.32*
Leaf expansion (d)	0.38	0.56*
Rates of herbivory		
Between-leaf variance†		
Seasonal	4.8	5.3
Annual	5.8	5.9
Between-plant variance		
Seasonal	38.2	41.1
Annual	23.2	26.7
Between-plant skewness		
Seasonal	1.26	1.28
Annual	1.53	1.26

* *P* < .05.

† Nested ANOVA on $\ln[(100 \times s^2_{ijk}) + 1]$, where s^2_{ijk} is the within-plant variance of the log-transformed grazing rate (see text). Values are weighted by the number of leaves per plant, although analysis without weighting gives similar results.

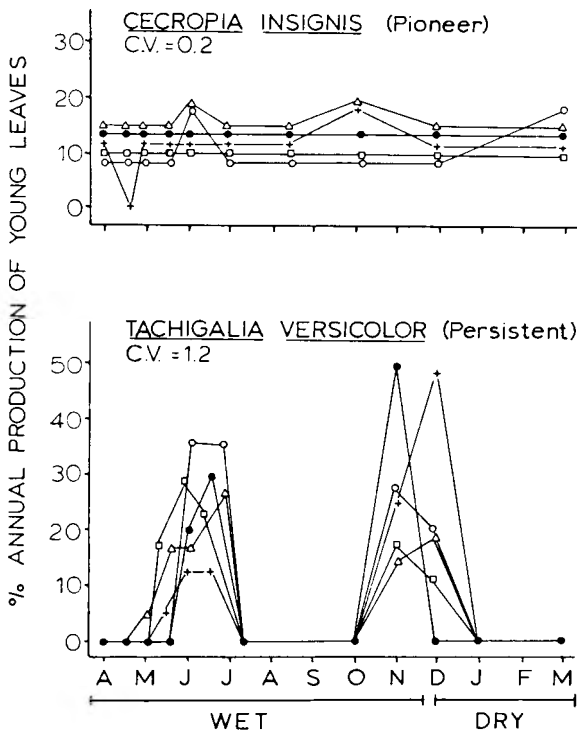


FIG. 4. Phenology of leaf emergence for *Tachigalia versicolor* and *Cecropia insignis*. Individual plants are represented by different symbols. cv is the coefficient of variation for the number of young leaves per plant each sample period.

coefficient of variation for the number of young leaves present each sample period (Fig. 5). Individuals of pioneer species have a significantly less synchronized emergence of young leaves throughout the year than do persistents ($P < .05$, Mann-Whitney U , Table 8). The amount of time necessary for an individual leaf to expand fully and to attain adult characteristics is significantly shorter for pioneer species ($P < .05$, Mann-Whitney U , Table 8).

Do these different patterns of leaf emergence for pioneers and persistents influence the distribution of grazing damage among leaves on a plant or among

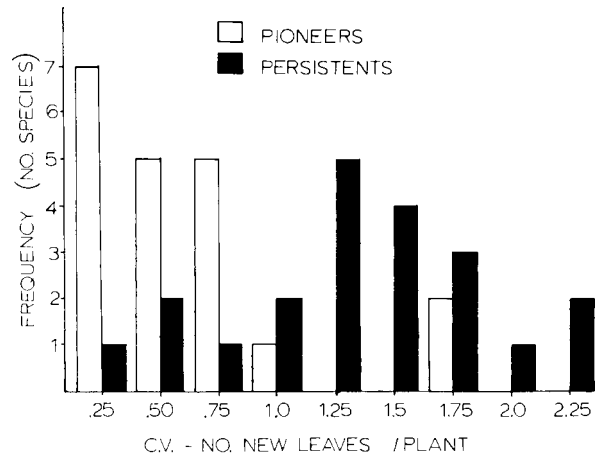


FIG. 5. Synchrony in leaf emergence for individual plants in 20 pioneer and 21 persistent species. Synchrony is expressed as the coefficient of variation (cv) for the number of young leaves per plant each sample period.

plants within a species? Although young pioneer leaves have shorter expansion times and are emerging throughout the year, the variance in damage among leaves on the same plant is no greater than the variance for young persistent leaves ($P > .7$, Table 8). It was hypothesized that the synchronized leaf emergence patterns for individuals of persistent species should lead to a high between-plant variance in damage. However, no differences were found between pioneer and persistent species with respect to either the between-plant variance or skewness for seasonal or annual estimates ($P > .4$, Table 8). Furthermore, neither expansion time nor flushing synchrony seems to reduce the average rates of herbivory. Expansion time is not significantly correlated with grazing, considering pioneer and persistents separately and together. The partial correlation of grazing and flushing synchrony, which has the effects of other defenses removed, is positive and significant ($P < .01$) for pioneers but not for persistents.

Growth rates

Annual growth rates were measured in terms of height and leaf production for 300 individuals. The average height growth rates for persistents are significantly lower than for pioneers ($P < .01$, Mann-Whitney U , Table 9). Pioneer species, on the average, grow 2.5 times as fast, and the maximum growth rate observed for an individual of each species is almost twice as high ($P < .01$, Mann-Whitney U , Table 9). Pioneer species produce more leaves per year, and since their leaves tend to be larger, the total leaf area produced is also substantially higher ($P < .01$).

Grazing rate on young and mature leaves for each species was regressed against annual height growth and leaf production. For most species, the regressions

TABLE 9. Annual growth rates for pioneer and persistent species. Differences tested by a Mann-Whitney U .

	Pioneers (n = 20)	Persistents (n = 21)
Number of plants	142	159
Height growth		
Mean (cm/yr)	96	37**
Maximum (cm/yr)	155	86**
Variance	3365	855**
Leaf production		
Number of leaves/yr	46	38
Leaf area (cm ² /yr)	6026	3700*

* $P < .05$; ** $P < .01$.

were based on eight plants, which may not be sufficient to identify trends, especially if the range of grazing damage was low. Only 3% of the regressions were significant ($P < .05$). The frequency of negative signs for the regression was compared for pioneers, persistents, and all species combined. Only grazing rate on mature leaves showed a significant negative relationship to leaf production ($P < .05$, chi-square), mostly due to the strong negative effect for persistents. In general, however, levels of herbivory did not have a demonstrable effect on growth.

The maximum growth rate for an individual in each species is an estimate of the potential growth rates under herbivory-free conditions. Since none of the study plants was entirely ungrazed, this is an underestimate, particularly for pioneer species. Maximum growth rates are positively correlated with nutritional content ($P < .02$) and negatively correlated with fiber measures ($P < .05$), toughness ($P < .02$), and phenols (NS). The only defense which has a positive relationship with maximum growth rates is pubescence on the lower leaf surface. Maximum growth is therefore negatively correlated with the general level of defense investment in mature leaves, and this is reflected in a significant positive correlation ($P < .007$) with grazing susceptibility.

DISCUSSION

Herbivory

Susceptibility to herbivory can be predicted from one important component of plant life history, the shade tolerance of saplings. Although there is a large range (3.5 orders of magnitude) in the average herbivory levels on mature leaves of different species, pioneers as a group are grazed six times more rapidly than persistent species. Since all plants were measured in light gaps, these differences in grazing are due primarily to between-species differences and not to habitat or herbivore availability.

These are the first field-collected results which examine herbivory as a function of plant life history. Other studies have approached this topic by determining food preference of generalist herbivores in the laboratory, but results are dependent on the herbivore used for testing (Grime et al. 1968, Cates and Oriens 1975, Otte 1975). Furthermore, it is impossible to predict damage levels in the field from laboratory results, because the relative pressures from specialist and generalist herbivores are unknown. Under natural conditions, the observed higher losses of early successional plants may not be due to many generalist herbivores but to heavy feeding by a few specialist species.

In addition to life history, leaf age strongly affects susceptibility to herbivores. In this study, young leaves suffer higher levels of herbivory than mature leaves for both pioneer and persistent species. Other investigators working under a range of laboratory and field

conditions have found similar results (Kennedy and Booth 1951, Dixon 1970, Feeny 1970, Reichle et al. 1973, Rockwood and Glander 1977, Hamilton et al. 1978, Ives 1978, Milton 1979, Coley 1980, Oates et al. 1980, but see Rhoades 1977a, b).

Defensive characteristics of leaves

Pioneer and persistent species differ dramatically in the defensive characters of mature leaves. Pioneer species exhibit the pattern suggested for unapparent plants (Feeny 1976, Rhoades and Cates 1976). They have lower levels of quantitative defenses such as phenols, fiber, and toughness and higher levels of nitrogen and water. Pubescence, generally considered a less expensive qualitative defense (Singh et al. 1971, Feeny 1976, Rhoades and Cates 1976, Van Dat et al. 1978), is more common in pioneers and may indicate the presence of other qualitative toxins. Persistents seem typical of apparent species. They have low damage levels, high concentrations of quantitative defenses, and are of poor nutritive value.

My data only partially support current ideas that young leaves are more nutritious and less well defended chemically and physically than mature leaves (McKey 1974, Rhoades and Cates 1976). In this study, young leaves of both pioneers and persistents are less tough and fibrous than mature leaves and have higher concentrations of nitrogen and water. However, the proposition that young leaves are poorly defended by quantitative chemicals (Feeny 1976, Rhoades and Cates 1976) was not supported by my work. Investigations of temperate species have found that young leaves have lower concentrations of quantitative defenses such as tannins, although they may have higher concentrations of qualitative toxins (Feeny 1970, Dement and Mooney 1974, Lawton 1976, Rhoades and Cates 1976, McKey 1979, but see Rhoades 1977a, b). Because of the problems of sequestering tannins away from cell machinery, it has been assumed that phenols are not practical defenses in young expanding leaves (Oriens and Janzen 1974, Feeny 1976, Rhoades and Cates 1976, McKey 1979). It is surprising that the young leaves in this study have two to three times the tannin concentrations found in mature leaves. Simple phenolics are relatively more common in young leaves than are condensed tannins, but both are present. In 85% of the species, young leaves have higher concentrations of total phenols. Young leaves of most species also have higher concentrations of condensed tannins (77% of the species for the Vanillin assay and 62% for the Leucoanthocyanin). Tannins may be more easily extracted from young than from mature leaves (Bate-Smith 1973, Mbi 1978, Oates et al. 1980), but the measured differences in phenol content between ages are large. Similar results have been noted for other tropical trees, suggesting that this phenomenon may be widespread. Total phenol levels in young leaves of various *Eucalyptus* species vary from 18 to 41% and levels of con-

densed tannins from 10 to 27% (Macauley and Fox 1980). These levels are comparable to the highest values found in my study. Data for eight tree species in an Indian rain forest show higher concentrations of both simple and condensed phenols in the young leaves (Oates et al. 1980). Milton (1979) found higher total phenol levels in young leaves from three of the four tree species tested from a neotropical forest. Concentrations of tannins and terpenoids are higher in the young leaves of two Leguminosae in Brazil (J. H. Langenheim, *personal communication*), and total phenols occur in higher concentrations in young leaves of several *Ingas* in Costa Rica (S. Koptur, *personal communication*). Although insufficient information exists on the frequency of quantitative chemicals in young leaves, these recent studies in tropical systems suggest that current views on the levels of chemical defense for young leaves should be revised.

Defenses and herbivory

This study is unique in simultaneously examining several major groups of leaf characteristics in order to determine their possible defensive role. Together these defenses explain 70–80% of the between-species variance in grazing damage on mature leaves, which suggests that they are among the major anti-herbivore defenses. Because they were examined simultaneously, it is possible through correlative statistics to estimate the relative effectiveness of each leaf character in reducing damage from all herbivores.

Although the role of chemical defenses against herbivores has received much attention (Feeny 1976, Rhoades and Cates 1976, Rosenthal and Janzen 1979), I found two structural aspects of leaves, toughness and fiber content, to be the most important correlates of grazing. These can be considered quantitative defenses with dosage dependent effects (Rhoades 1979). Toughness has been shown to deter herbivores (Tanton 1962, Grime et al. 1968, Feeny 1970, Rhoades 1977b, Rausher and Feeny 1980), but its general importance has not been widely recognized. There is evidence from ruminants that fiber content, and particularly the lignin component, reduces the digestibility of plant material by increasing indigestible bulk and by hydrogen bonding with carbohydrates and proteins (Burns et al. 1972, Burns and Cope 1974, Van Soest 1975, Swain 1979). The possible role of fiber as a defense in natural communities has been examined only recently for nonruminants (Milton 1979, Oates et al. 1980) and never for insects. In mammals, fiber digestibility increases with body size due to increased gut retention times (M. L. Demment and P. J. Van Soest, *personal communication*). For small mammals and perhaps insects, fiber content may therefore present more of a barrier.

Plant secondary compounds, and particularly phenols, have been considered as major defenses against

herbivores (Whittaker and Feeny 1971, Rhoades 1979). This view of phenols is based primarily on laboratory studies showing an inhibitory effect of tannins on herbivores (Feeny 1968) or on field studies which focused on the effects of phenols and not on their relative importance as compared to other defenses (Feeny 1970, Rhoades 1977a, b, Gartlan et al. 1978, McKey et al. 1978). It is therefore surprising that for mature leaves in this study, phenol measures are the least well correlated with herbivory. Similarly, no correlation was found between phenol content and grazing damage for ferns (Balick et al. 1978) or for several species of trees (Fox and Macauley 1977, Milton 1978, Morrow and Fox 1980, Oates et al. 1980). This evidence suggests that the importance of phenolic content as a defense may have been over emphasized.

For young leaves, phenols are not significantly correlated with grazing, but the high phenol levels suggest that they may be relatively more important than in mature leaves. This seems reasonable given that young leaves do not have high fiber contents or toughness. The presence of phenols in mature leaves may result partially from high concentrations in young leaves and slow turnover rates.

Leaf protein is correlated with herbivore food choice in the field (Onuf et al. 1977, Onuf 1978, Milton 1979, McClure 1980, Morrow and Fox 1980), and in laboratory studies nitrogen and water contents are positively related to larval growth rates for several taxonomic orders of insects (House 1967, Horsefield 1977, Scriber 1977, Slansky and Feeny 1977, Reese and Beck 1978, Scriber and Feeny 1979, McClure 1980, but see Schroeder and Malmer 1980). The low nutritive quality and low grazing rates on mature persistent leaves supports these observations. Conversely, the high concentrations of water and nitrogen in young leaves of this study may be an important reason why they were grazed more heavily than mature leaves.

Pubescence is positively correlated with herbivory. This is probably not due to a direct positive effect of hairs on herbivores, because an increase in pubescence within agricultural crops reduces grazing (Parnell et al. 1945, Painter 1958, Sikka et al. 1966, Singh et al. 1971, Levin 1973, Sen Gupta and Miles 1975); rather, it may be due to the negative correlation with more effective defenses. Pubescence therefore appears to be the best single, readily observed character for identifying poorly defended leaves or plants.

Defensive characteristics are correlated with life history and habitat to a greater extent than with phylogenetic relationships. Pioneer and persistent members in the same family are not clustered by multivariate analyses of defenses on mature leaves. This dissimilarity between related species may occur because the quantitative defenses measured in this study are taxonomically widespread (Whittaker and Feeny 1971, Rhoades 1979). Taxonomic similarities might be more obvious in detailed biochemical studies which

also examined qualitative toxins (e.g., Cates and Rhoades 1977).

Temporal distribution and herbivory

The phenology of leaf emergence can be examined as the degree of synchrony (1) within an individual plant, (2) between individuals within a species, and (3) between species in a community. All three levels of synchrony could influence herbivory potentially. Although it has been suggested that plants may satiate herbivores through synchronous emergence of leaves both within and between plants (Feeny 1970, McKey 1974, Rhoades and Cates 1976), the temporal availability of young leaves and resultant effects on herbivory have not been quantified (but see Feeny 1970, Futuyma and Wasserman 1980).

The advantages of synchronous leaf emergence suggested by McKey (1974) are not supported by my study. Young leaves of persistent species emerge more synchronously within a plant, within a species, and within the community as a whole than do pioneer leaves, yet they suffer similar damage levels. Since at any one time all or none of the young leaves on a particular persistent individual are at an appropriate age to be eaten, one would expect a high between-plant variance. Similarly, because pioneer leaves emerge throughout the year, it was expected that each leaf would be grazed by a different array of herbivores. This, coupled with shorter expansion times, should lead to a higher between-leaf variance in damage on pioneers as compared to persistents. However, the degree of synchrony does not appear to alter dispersion of damage and is positively correlated with grazing rates. In fact, synchronous emergence may be costly to the plant in terms of lost productivity, particularly in a habitat such as light gaps where competition is intense and rapid growth is important. Since productivity rates are lower in the shaded understory than in gaps, the relative cost of waiting to flush leaves synchronously at one time of year would not be as great. Furthermore, young persistent leaves may gain some advantage by emerging at the beginning of the rainy season (Coley 1982) when herbivore populations are lowest (Wolda 1978) and nutrient availability highest.

Spatial distribution and herbivory

In models of plant apparency, the degree to which a species escapes discovery by herbivores is considered the major factor influencing the evolution of plant defenses. To test this idea, one must first define escape and identify the processes by which it might influence selection for defenses. The discovery patterns of herbivores are assumed to be independent of between-plant differences in defenses. In this undiscovered portion of the population, poorly defended individuals which do not have the costs of producing defenses will be at a selective advantage. Escape due to random search patterns of herbivores can thus cause differ-

ential selection for defenses in different subgroups of the population (Levene 1953, Wallace 1968, 1975, Christiansen 1975). A population which is positively skewed with respect to herbivory will have a large subgroup of individuals selected for lower defenses and only an extreme upper tail with strong selection for defenses. Hence, the more positively skewed a population is for herbivory, the greater the intensity of selection for reduced defenses. Random search patterns would also lead to a high variance in herbivory, since some individuals would avoid damage and others would be discovered and heavily grazed. The greater the variance in damage due to herbivore discovery patterns, the lower the intensity of selection on defenses, and the slower the rate of evolution. I therefore suggest that intraspecific variance and skewness in herbivory among individuals be used as indices for quantifying the extent to which a population is "escaping" damage from herbivores. Ideally, initial patterns of discovery by herbivores should be distinguished from subsequent decisions to feed, but in most field situations, this is impractical.

There are several factors which might influence these indices of grazing dispersion among individuals in a population. First, the spatial distribution of plants has been considered the major component regulating the discovery patterns of herbivores (Feeny 1976, Rhoades and Cates 1976). Patchily distributed plants are considered unapparent to herbivores and are expected to escape discovery more easily. Since herbivores have evolved host-finding capabilities, this cannot be tested except in the present ecological context.

Second, the relative proportions of specialists and generalists feeding on a species could affect dispersion of damage. Specialist herbivores have detoxification mechanisms for the chemical defenses of their host plants (Krieger et al. 1971), so once on a plant, there are no dietary reasons for leaving. This might cause high damage levels on plants with herbivores relative to those without, creating a large between-plant variance. It is suggested that detoxification mechanisms of generalist herbivores are adapted to handle low concentrations of a range of chemical defenses (Freeland and Janzen 1974, Wasserman 1979), so it is expected that feeding patterns would include several plant species to minimize intake of any particular chemical defense (Freeland and Janzen 1974). If generalists are indeed more mobile than specialists, they should cause a more even distribution of damage among individuals of a particular species.

A third factor which could influence damage dispersion is the within-population variation in defensive characters. A high variance in defenses between individuals would increase both the variance and skewness of herbivory in the population. Unlike the previous two factors where the influence on damage dispersion was random with respect to the genetic make-up of individuals, this third effect is based on

phenotype differences in defense. Levels of defense have been shown to differ among conspecific individuals, affecting food preferences of herbivores (e.g., Jones 1962, 1972, Cates 1975, Cooper-Driver et al. 1977, Rhoades 1977a) and causing frequency-dependent selection on plant defenses (Daday 1954, 1965, Sturgeon 1979).

No previous studies have examined the distribution of damage among individuals as a measure of escape. A few studies have tried to quantify escape in terms of mean damage levels and to determine important causal factors. They have examined herbivory as a function of conspecific density and neighborhood diversity (Pimentel 1961a, b, Thompson and Price 1974) but have obtained conflicting results.

Using the life history dichotomy between pioneer and persistent species, I compared grazing dispersion and spatial patterning of the two groups in order to evaluate the importance of escape. On the basis of apparency theories, one would expect pioneers to exhibit more evidence of escape than persistents owing to differences in their life history and defensive characteristics.

To quantify patterns of escape, I measured the distribution of damage within a species as (1) the skewness in grazing rates among individuals, and (2) the between-plant component of variance in grazing. Persistent species tend to have a more skewed distribution and pioneer species a greater between-plant variance. As was mentioned earlier, there are at least three factors which might contribute to these patterns: the spatial distribution of plants, the degree of herbivory by specialists, and the between-plant variation in defenses.

The spatial distribution of pioneers and persistents in gaps is similar and probably does not influence the distribution of damage among plants. There is no significant difference in either the density or distribution of pioneer and persistent individuals among gaps, and clumping within gaps does not significantly affect grazing under natural or manipulated conditions. However, since pioneer species only occur in gaps and not throughout the understory, the foraging behavior of herbivores becomes important. There is evidence that insects are capable of concentrating their search efforts in gaps (Benson et al. 1976, Benson 1978, R. E. Silberglied, *personal communication*). If it requires little effort to find a gap relative to the total searching budget of a herbivore, pioneers and persistents would appear equally patchy. This suggests that predictions as to the apparency or distribution of plants based on life history characteristics or growth form should be approached with caution.

Despite the higher variance in damage for pioneers, the average positive skewness in damage is less than for persistent populations. This indicates that only a small proportion of each pioneer population has low levels of herbivory and is under selection for reduced

defenses. This suggests that pioneers have less potential for escape than persistents. It is therefore unlikely that the low defense levels of pioneer species are an adaptive response to spatial escape from herbivores.

It is also unlikely that the distribution in grazing damage among individuals is due to the between-plant variation in defenses. There is no evidence suggesting that pioneers show more within-species variation in defenses than persistents. In addition to a higher between-plant variance, pioneers have a higher variance between leaves on the same plant, which supports the idea that they may be grazed primarily by specialists. There is evidence that the quantitative defenses seen in persistents lead primarily to grazing by generalists (Otte 1975, Futuyma 1976, Rhoades and Cates 1976), causing a more even distribution of damage among plants. I therefore suggest that pioneers and persistents are equally easy for herbivores to discover and that the higher between-plant variance in grazing damage for pioneers is due to feeding by specialist herbivores.

Growth and defense

Antiherbivore defenses must represent an energetic and nutritive cost to the plant (Chew and Rodman 1979, Rhoades 1979). These resources are therefore not available for growth and reproduction (Hanover 1966, Foulds and Grime 1972, Mothes 1976, Pimentel 1976, Tester 1977). This hypothesized tradeoff between investments in growth and defense is manifest in pioneer and persistent species, with pioneers apparently allocating resources to growth and persistents to defense. Pioneers suffer levels of herbivory on mature leaves six times higher than those on persistents, yet they grow >2.5 times as fast. The fact that they are able to tolerate high herbivory suggests they are producing less expensive or less valuable leaves. Consistent with this hypothesis is the finding that pioneer leaves have lower concentrations of fiber and phenols, are less tough, and have shorter leaf lifetimes. Pioneers also have higher maximum growth rates. Since growth potential is negatively correlated with quantitative defenses for pioneers and persistents separately and combined, it may be an indirect measure of the cost of these defenses.

CONCLUSIONS

There is no evidence that pioneers have the potential to escape discovery by herbivores as measured by plant distribution in gaps or by the mean and dispersion of grazing damage under experimental or natural conditions. Pioneer species, however, exhibit lower levels of quantitative defenses as predicted for unapparent plants. Persistent species have high levels of fiber, phenols, and toughness typical of apparent plants. This suggests that these differences in defensive characters between the two life histories are not due to a greater ability of pioneers to escape discovery as pre-

dicted by the apparency model. Instead, I hypothesize that pioneer species are simply able to tolerate high rates of herbivory because of cheaper leaves and faster growth rates. For a given rate of herbivory, in terms of leaf area removed, the impact on pioneers will be less than for persistents since the cost of production and maintenance of a pioneer leaf is also less. Although escape may be important in some environments, it does not appear to be a necessary prerequisite for the evolution or success of poorly defended plants.

I suggest that the maximum potential productivity of different habitats will favor plant species with different levels of defense. Productivity in the understory is lower than in gaps because light levels are greatly reduced and nutrients are less available (Leigh et al. 1982). Consequently, a leaf in the understory has a lower return from photosynthesis than a leaf surviving the same length of time in a light gap. Although rates of leaf removal are comparable for species growing in both gap and understory sites (Coley 1981, 1983), the impact of herbivory on plants would be greater in the understory. Since poorly defended pioneers are eaten rapidly, leaves on individuals growing in the understory would have low levels of total production. These low levels may be a reason why pioneer saplings are absent in the understory, although many species are capable of germinating there (Garwood 1979). However, with the high rates of productivity possible in light gaps, pioneers can grow fast enough to tolerate the levels of herbivory on Barro Colorado Island. The well-defended and long-lived leaves of persistent species may allow them to exist in the low-quality understory.

As an alternative to the apparency model, I propose that habitat quality is a major selective force behind the evolution of different defensive systems (see also Bryant and Kuropat 1980, Bryant and Chapin, *in press*). High-quality habitats are defined as environments in which rapid growth is possible, as opposed to low-quality ones where growth is limited by any abiotic factor, such as light or micronutrients. For a given level of herbivore pressure, the advantage of defense should increase as the potential maximum growth rate declines. Because of the apparent tradeoff between growth and defense, poorly defended species should be favored when habitat quality and growth potential are high relative to herbivory. Under these conditions, it would be possible for undefended species to "tolerate" herbivory if the reduction in productivity due to losses was less than the alternative costs of defense. Low defense levels are only possible if herbivore populations do not increase indefinitely in response to food availability but are partially limited by other factors such as predators. In habitats with low growth potential or high herbivory, the relative losses to herbivory are potentially greater, and well-defended species would be at a competitive advantage.

This theory proposes that habitat quality determines the type and extent of plant commitment to antiherbivore defenses. In areas where water, light, or nutrients are limiting, there will be selection against poorly defended plants. This is supported by information from tropical forests on nutrient-poor soils, where poorly defended (McKey et al. 1978) and fast-growing species (Brunig 1969, Janzen 1974, P. D. Coley, *personal observation*) are completely absent. Inherently slower growth rates are also found for grass species from infertile rather than fertile sites (Bradshaw et al. 1964) and for *Eucalyptus* populations from dry rather than wet areas (Parsons 1968). In addition to large-scale differences between habitats, the heterogeneity of most environments provides both high- and low-quality sites for growth. I expect, therefore, that the defensive characters of different species in a single community should parallel differences in the quality of their preferred microsites. The higher levels of defense seen for late than for early successional plants or for trees than for herbs (Feeny 1976, Rhoades and Cates 1976) may be the result of microsite quality and not plant apparency. The proposed relationship between habitat quality and plant defense is consistent with these community level patterns and may provide a partial explanation for within- and between-habitat variation in plant defensive systems.

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Lignin = lignin (% dry mass); Cell = Cellulose (% dry mass); Tough = toughness (newtons); Hair. u = density of hairs/mm² on upper leaf surface; Hair. l = density of hairs/mm² on lower leaf surface; Water = % water; N2 = total nitrogen (% dry mass); Growth = annual change in height (cm); Gmax = maximum annual height growth for an individual (cm); Lfarea = annual leaf area production (cm²); Dist = spatial distribution of plants. Lloyd's (1967) patchiness index; Expan = no. days from bud to maturity for young leaves; Flush = synchrony of leaf emergence. CV for the number of young leaves per plant each sample period.

Species	Mature leaves								
	Tough	Hair. u	Hair. l	Water	N2	Growth	Gmax	Lfarea	Dist
Anacardiaceae									
<i>Spondias radlkoferi*</i>	3.61	0.0	0.0	81	2.65	42	73	4448	2.7
Annonaceae									
<i>Annona spraguei*</i>	5.09	1.8	14.0	66	2.20	116	171	8162	8.1
<i>Desmopsis panamensis</i>	7.64	0.0	3.0	64	2.21	4	60		
<i>Guatteria dumentorum</i>	5.23	0.0	2.0	62	2.35	74	120	6968	5.9
Apocynaceae									
<i>Aspidosperma megalocarpon</i>	11.56	0.0	0.0	58	1.29	22	44	3007	20.4
Bignoniaceae									
<i>Jacaranda copaifera*</i>	2.48	0.0	0.0	66	2.34	51	90	5052	3.7
<i>Tabebuia rosea*</i>	5.71	0.0	0.0	74	2.34	47	144	1445	2.4
Bombacaceae									
<i>Ochroma pyramidale*</i>	3.14	0.0	18.0	67	2.23	475	998		
<i>Quararæbea asterolepis</i>	4.77	0.0	0.0	63	2.46	20	44	1725	3.8
Boraginaceae									
<i>Cordia alliodora*</i>	3.18	0.6	0.6	67	3.10	23	67	310	15.9
Burseraceae									
<i>Protium tenuifolium</i>	6.35	0.0	0.0	53	1.71	39	78	2710	4.5
<i>Tetragastris panamensis</i>	6.36	0.0	0.0	49	1.56	27	69	2133	3.1
<i>Trattinickia aspera*</i>	2.46	0.0	0.0	65	2.23	127	270	11 210	11.6
Caesalpinioideae									
<i>Prioria copaifera</i>	7.17	0.0	0.0	56	2.15	3	16	302	28.8
<i>Swartzia simplex</i>	12.02	0.0	0.0	56	2.59	1	30		
<i>Tachigalia versicolor</i>	5.80	0.0	0.0	55	2.26	51	87	9575	5.2
Chrysobalanaceae									
<i>Hirtella triandra</i>	5.13	0.0	0.3	59	1.81	45	58	4003	3.9
Euphorbiaceae									
<i>Alchornea costaricense*</i>	5.55	0.0	0.0	66	2.32	62	103	2026	4.5
<i>Croton bilbergianus*</i>	3.99	0.0	11.0	77	2.71	91	205		
<i>Hyeronima laxiflora*</i>	3.02	0.3	0.2	78	2.43	49	102	9807	7.4
<i>Sapium caudatum*</i>	4.92	0.0	0.0	82	3.05	69	156	4323	12.5
Flacourtiaceae									
<i>Casearea arborea*</i>	2.73	0.0	0.0	69	2.82	95	138	14 625	9.5
<i>Zuelania guidonia*</i>	4.92	0.6	1.4	71	1.99	76	118	9755	13.2
Guttiferae									
<i>Calophyllum longifolium</i>	11.56	0.0	0.0	64	1.17	59	101	2420	10.9
Melastomataceae									
<i>Miconia argentea*</i>	3.84	0.0	18.0	66	1.67	118	184	9420	4.4
Meliaceae									
<i>Guarea glabra</i>	5.76	0.0	0.0	69	3.10	63	115	3303	3.1
<i>Guarea multiflora</i>	6.56	0.0	0.6	62	2.40	37	71	3866	3.4
<i>Trichilia cipo</i>	5.79	0.0	0.0	60	2.06	41	105	1101	4.4
Moraceae									
<i>Cecropia insignis*</i>	5.79	0.0	16.0	70	2.08	117	316	5131	6.4
<i>Cecropia obtusifolia*</i>	2.82	0.6	16.0	74	2.95	126	235	9484	7.3
<i>Poulsenia armata</i>	7.20	0.0	0.0	64	1.60	51	118	5420	4.2
Myristicaceae									
<i>Virola sebifera</i>	4.51	0.0	3.4	68	2.71	51	66	2800	9.4
Rubiaceae									
<i>Alseis blackiana</i>	2.73	0.0	0.0	69	2.97	73	160	6837	3.7
<i>Faramea occidentalis</i>	6.50	0.0	0.0	60	1.61	1	38		
<i>Macrocnemum glabrescens</i>	3.67	0.0	1.4	77	2.35	12	73	4894	16.2
Rutaceae									
<i>Zanthoxylum belizense*</i>	3.06	0.4	2.0	73	2.68	82	260	6349	16.4
<i>Zanthoxylum panamense</i>	3.19	0.0	0.0	69	2.82	59	141	1041	11.6
Sapindaceae									
<i>Cupania fulvida*</i>	7.09	0.6	0.6	57	1.87	51	66	6968	7.8
<i>Cupania sylvatica</i>	5.39	0.0	0.0	62	2.57	35	91	4331	7.5
Sapotaceae									
<i>Cvanodendron panamense</i>	9.36	0.0	0.0	63	1.80	51	91	2152	4.3
<i>Pouteria unilocularis</i>	5.05	0.0	0.0	57	2.92	25	60	2202	2.0
Simaroubaceae									
<i>Simarouba amara</i>	4.99	0.0	0.0	66	2.36	48	93	6910	8.6
Tiliaceae									
<i>Apeiba membranacea*</i>	3.06	0.8	1.2	69	2.19	49	104	1640	3.9
<i>Apeiba tibourbou*</i>	3.15	0.8	0.8	74	2.64	68	116	3324	3.7
<i>Luehea seemannii*</i>	3.01	0.8	16.0	59	2.62	45	90	2632	6.0
Ulmaceae									
<i>Trema micrantha*</i>	2.51	0.0	0.0	66	2.89	132	300	4403	28.1

APPENDIX

Continued.

Species	Young leaves						
	Grazing	Phenol	Vanil	Leuco	NDF	ADF	Lignin
Anacardiaceae							
<i>Spondias radlkoferi*</i>	1.585	159.9	6.1	9.5	29.5	10.3	1.9
Annonaceae							
<i>Annona spraguei*</i>	0.760	29.4	2.1	1.3	46.8	24.6	8.8
<i>Desmopsis panamensis</i>	0.783	104.8	11.7	30.7	38.3	30.6	11.4
<i>Guatteria dumentorum</i>	0.410	198.7	79.4	152.2	48.0	45.1	16.0
Apocynaceae							
<i>Aspidosperma megalocarpon</i>	1.487	103.2	0.3	1.3	39.8	26.3	11.4
Bignoniaceae							
<i>Jacaranda copaifera*</i>	0.291	110.2	1.2	3.1	34.0	23.5	11.7
<i>Tabebuia rosea*</i>	2.783	29.5	5.4	13.0	46.7	40.4	11.4
Bombacaceae							
<i>Ochroma pyramidale*</i>	0.178	219.1	122.0	119.2	48.9	52.4	24.7
<i>Quararëba asterolepis</i>	1.035	64.1	23.5	32.9	58.1	29.3	10.1
Boraginaceae							
<i>Cordia alliodora*</i>	0.337	163.8	0.6	0.0	45.3	37.4	15.1
Burseraceae							
<i>Protium tenuifolium</i>	1.483	175.0	59.2	153.6	37.6	29.8	14.0
<i>Tetragastris panamensis</i>	1.706	238.3	11.8	25.8	25.9	18.5	7.0
<i>Trattinickia aspera*</i>	0.070	230.3	1.9	3.7	19.9	14.7	3.0
Caesalpinioideae							
<i>Prioria copaifera</i>	0.781	370.2	158.3	33.2	45.1	27.2	8.6
<i>Swartzia simplex</i>	2.504	11.8	0.8	0.1	53.2	30.5	6.5
<i>Tachigalia versicolor</i>	1.084	292.6	118.1	212.7	40.2	28.7	10.8
Chrysobalanaceae							
<i>Hirtella triandra</i>	1.444	210.1	86.1	196.3	39.6	45.5	16.9
Euphorbiaceae							
<i>Alchornea costaricensis*</i>	1.571	378.0	0.8	0.6	13.7	9.2	0.9
<i>Croton bilbergianus*</i>	0.310	32.7	1.9	0.1	43.7	25.1	6.4
<i>Hycronima laxiflora*</i>	0.586	224.0	76.4	252.7	38.9	37.4	16.6
<i>Sapium caudatum*</i>	0.679	154.6	0.8	0.6	24.6	17.3	3.4
Flacourtiaceae							
<i>Casearea arborea*</i>	0.427	66.3	3.7	1.8	41.6	24.0	9.8
<i>Zuelania guidonia*</i>	0.147	116.7	4.5	1.0	32.0	19.0	5.7
Guttiferae							
<i>Calophyllum longifolium</i>	0.358	244.3	115.1	145.7	48.4	44.2	15.1
Melastomataceae							
<i>Miconia argentea*</i>	0.156	77.5	8.2	18.4	32.1	26.9	11.6
Meliaceae							
<i>Guarea glabra</i>	1.034	190.9	72.4	135.4	44.0	39.2	14.5
<i>Guarea multiflora</i>	1.182	225.0	76.6	145.6	40.9	41.0	12.9
<i>Trichilia cipo</i>	0.909	313.0	105.1	195.3	40.3	43.6	18.3
Moraceae							
<i>Cecropia insignis*</i>	0.155	130.8	40.1	77.7	42.2	41.1	7.7
<i>Cecropia obtusifolia*</i>	0.540	46.1	5.2	10.0	46.6	33.4	12.2
<i>Poulsenia armata</i>	0.021	48.9	1.9	1.2	37.5	22.8	6.2
Myristicaceae							
<i>Virola sebifera</i>	0.509	145.0	13.3	24.5	54.8	32.3	14.1
Rubiaceae							
<i>Alseis blackiana</i>	0.309	162.8	3.3	10.1	41.7	27.5	12.4
<i>Faramca occidentalis</i>	0.064	13.0	3.6	22.0	36.4	27.8	7.2
<i>Macrocnemum glabrescens</i>	0.583	219.6	58.1	246.6	61.8	55.8	14.1
Rutaceae							
<i>Zanthoxylum belizense*</i>	0.863	103.7	23.5	42.1	49.6	32.4	14.6
<i>Zanthoxylum panamense</i>	1.232	141.9	1.2	0.5	26.1	7.4	1.4
Sapindaceae							
<i>Cupania fulvida*</i>	1.642	169.9	83.9	159.0	47.9	43.3	12.5
<i>Cupania sylvatica</i>	1.006	17.1	2.6	3.4	32.7	20.2	5.1
Sapotaceae							
<i>Cyanodendron panamense</i>	0.448	159.0	35.9	65.9	31.6	41.4	21.5
<i>Pouteria unilocularis</i>	1.114	121.8	46.2	53.8	36.6	26.6	13.0
Simaroubaceae							
<i>Simarouba amara</i>	0.697	389.1	4.4	5.7	17.5	9.3	1.6
Tiliaceae							
<i>Apeiba membranacea*</i>	0.535	72.7	0.4	0.1	41.7	28.1	11.1
<i>Apeiba tibourbou*</i>	0.348	69.0	0.5	0.0	62.5	31.0	12.2
<i>Luehea seemannii*</i>	0.869	106.9	43.1	43.3	45.3	38.0	17.7
Ulmaceae							
<i>Trema micrantha*</i>	0.421	101.7	21.3	42.6	21.7	18.6	3.6

APPENDIX

Continued.

Species	Young leaves							
	Cell	Tough	Hair, u	Hair, l	Water	N2	Expan	Flush
Anacardiaceae								
<i>Spondias radlkoferi*</i>	8.4	2.52	0.0	0.0	82	3.01	27	0.97
Annonaceae								
<i>Annona spraguei*</i>	15.5	1.50	6.0	16.0	76	2.77	26	0.80
<i>Desmopsis panamensis</i>	18.9	2.94	0.0	10.0	81	4.23	44	
<i>Guatteria dumentorum</i>	29.0	1.54	6.7	7.3	77	2.67	40	0.82
Apocynaceae								
<i>Aspidosperma megalocarpon</i>	14.2	2.52	0.0	0.0	80	2.34	30	1.49
Bignoniaceae								
<i>Jacaranda copaifera*</i>	11.8	1.96	0.0	0.0	67	3.42	38	0.31
<i>Tabebuia rosea*</i>	28.6	1.24	0.0	0.0	83	3.70	40	1.76
Bombacaceae								
<i>Ochroma pyramidale*</i>	25.1	1.94	4.0	18.0	72	2.48	38	
<i>Quararæba asterolepis</i>	18.6	1.79	0.0	0.0	80	3.66	50	1.96
Boraginaceae								
<i>Cordia alliodora*</i>	21.8	1.57	1.0	1.2	73	3.50	30	0.60
Burseraceae								
<i>Protium tennuifolium</i>	15.7	2.83	0.0	0.0	74	3.35	49	1.34
<i>Tetragastris panamensis</i>	11.5	1.70	0.0	0.0	73	2.08	51	1.25
<i>Trattinickia aspera*</i>	11.4	1.39	0.0	0.0	68	3.24	29	0.65
Caesalpinioideae								
<i>Prioria copaifera</i>	18.6	2.09	0.0	0.0	79	3.25	37	2.07
<i>Swartzia simplex</i>	22.8	3.82	0.0	0.0	81	4.38	50	
<i>Tachigalia versicolor</i>	17.6	1.54	0.0	0.3	72	3.73	40	1.18
Chrysobalanaceae								
<i>Hirtella triandra</i>	26.9	2.16	0.4	0.3	76	2.30	47	1.42
Euphorbiaceae								
<i>Alchornea costaricensis*</i>	7.4	1.61	0.0	0.0	70	3.09	38	0.91
<i>Croton bilbergianus*</i>	17.1	2.66	2.0	12.0	80	4.54	53	
<i>Hyeronima laxiflora*</i>	20.6	1.92	1.3	2.2	75	2.73	38	0.26
<i>Sapium caudatum*</i>	13.9	3.81	0.0	0.0	81	4.25	28	0.73
Flacourtiaceae								
<i>Casarea arborea*</i>	13.3	2.10	0.0	0.0	77	4.31	26	0.71
<i>Zuelania guidonia*</i>	12.8	1.60	3.9	8.5	72	2.61	38	0.40
Guttiferae								
<i>Calophyllum longifolium</i>	29.1	2.92	0.0	0.0	80	1.83	36	0.96
Melastomataceae								
<i>Miconia argentea*</i>	14.5	3.14	7.0	16.0	69	2.07	91	0.40
Meliaceae								
<i>Guarea glabra</i>	24.6	3.55	0.0	0.0	78	4.18	41	1.56
<i>Guarea multiflora</i>	27.9	3.01	0.3	2.2	77	4.03	65	1.62
<i>Trichilia cipo</i>	24.0	2.58	0.0	0.0	69	2.75	49	1.69
Moraceae								
<i>Cecropia insignis*</i>	29.2	4.53	0.0	16.0	78	2.41	18	0.15
<i>Cecropia obtusifolia*</i>	16.7	2.29	1.5	16.0	80	3.71	17	0.21
<i>Poulsenia armata</i>	16.2	4.74	0.0	0.0	88	3.66	43	1.31
Myristicaceae								
<i>Virola sebifera</i>	18.1	1.95	4.3	6.2	75	3.21	67	0.79
Rubiaceae								
<i>Alseis blackiana</i>	14.8	2.33	0.4	0.0	73	3.99	60	0.90
<i>Faramea occidentalis</i>	20.2	2.22	0.0	0.0	83	2.17	55	
<i>Macrocnemum glabrescens</i>	41.6	1.73	0.0	2.9	80	2.19	42	0.86
Rutaceae								
<i>Zanthoxylum belizense*</i>	17.2	2.22	1.1	4.9	74	4.22	37	0.39
<i>Zanthoxylum panamense</i>	5.9	1.73	0.0	0.0	74	4.34	44	0.52
Sapindaceae								
<i>Cupania fulvida*</i>	30.4	3.23	2.8	3.2	63	2.33	50	1.56
<i>Cupania sylvatica</i>	14.8	2.15	0.0	0.0	73	4.87	38	2.07
Sapotaceae								
<i>Cyanodendron panamense</i>	19.0	3.22	0.0	4.8	66	2.42	33	1.03
<i>Pouteria unilocularis</i>	13.6	2.94	0.0	0.0	78	5.11	32	2.00
Simaroubaceae								
<i>Simarouba amara</i>	7.7	2.48	0.0	0.0	73	3.36	40	0.50
Tiliaceae								
<i>Apeiba membranacea*</i>	15.2	1.72	6.7	8.0	72	2.67	23	0.69
<i>Apeiba tibourbou*</i>	18.8	1.88	4.0	3.0	79	2.87	23	0.82
<i>Luehea seemannii*</i>	19.6	1.61	1.9	16.0	70	3.18	31	0.72
Ulmaceae								
<i>Trema micrantha*</i>	13.0	2.17	0.0	0.0	74	3.09	34	0.74