Rates of Herbivory on Different Tropical Trees

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ABSTRACT

Rates of herbivory on marked young and mature leaves from saplings of 21 canopy tree species were measured in the wet and dry seasons. Species were classified into two life history groups: persistent species which are found throughout the shaded understory, and pioneer species which only become established in light gaps created by fallen trees. Mature leaves of slow-growing persistent species were eaten by insects at an average annual rate of 21%, whereas rapidly growing pioneer species were grazed 4 times faster in the dry season and 10 times faster in the wet. In general, young leaves suffered higher rates of damage than mature leaves, with rates being an order of magnitude higher for persistent species. The higher variance between plants and low variance between leaves on the same plant in grazing damage for young persistent leaves suggests that their synchronous emergence at the beginning of the rains might satiate herbivores. There is no evidence that the patchy occurrence of pioneer plants only in light gaps leads to spatial escape from herbivores.

INTRODUCTION

How does grazing damage differ from season to season and from one species of tree to another? How much more rapidly are young leaves eaten than old ones? Are leaves of colonizing species eaten more than those of mature forest trees? This information will help us understand how different trees cope with herbivory and will shed light on the seasonal rhythms in the abundance and behavior of herbivores.

METHODS

The Data

I selected saplings of 21 species of canopy trees in order to measure rates of leaf consumption: 8 species of pioneers, which are fast-growing and shade-intolerant, and whose saplings only occur in sunny openings, and 13 species of persistents, which can germinate in the shade and either grow or persist suppressed in the understory until a gap opens in the canopy above (Foster and Brokaw, this volume). I selected these species according to their abundance as adults in the forest canopy on Barro Colorado and as saplings in clearings opened there by the fall of canopy trees.

I selected plants between 0.5 and 2 m tall, whose leaves were within reach, in treefall gaps less than three years old. Such light gaps are important centers of forest regeneration (Aubreville, 1971; Bray, 1956; Hartshorn, 1978; Jones, 1945; Schulz, 1960; Brokaw, this volume). I marked one set of 206 plants in the wet season, May and June of 1977, and another set of 143 plants in the dry season, February and March of 1979. I tagged an average of eight leaves per plant, including some leaves just emerging from the bud and a few of the mature leaves. I measured the total area of each tagged leaf and the total area of holes and damaged surfaces by placing a clear plastic grid (400 squares per square inch) over the leaf and counting the squares over the relevant areas. I measured damaged areas and total leaf area when tagging the leaves and again at a later time, 25 days later in the dry season, and every 14 days for up to three months in the rainy season.

The majority of the damaged areas I considered were caused by leaf consumption by insects. These were either holes, mines, galls, or scraped surfaces. However, I also included necrotic areas which may have been caused by microbial or fungal infection or by tissue death resulting from grazing. Herbivores chewed some leaves off at the petiole even though portions of the leaf blade remained, and the plants dropped other leaves, presumably because they were excessively damaged. There were a few cases of mammal grazing, easily distinguished by teeth marks: these were excluded from the analysis.

The Analysis

For each leaf, I calculated consumption rate as the percentage of area eaten per day, that is, the change during the sampling period in the percentage of the leaf's area devoted to holes, divided by the number of days of observation. Holes of known area punched in 105 young leaves grew with the leaves, so that the proportion of leaf area taken up by the holes did not change significantly as the leaves expanded ($r^2 = 0.88$). Expressing consumption as a rate and not as a single measure of standing crop also corrects for differences in leaf lifetimes.

Grazing damage is clumped, varying from leaf to leaf on the same plant and from plant to plant in the same species. I measured the first by the variance in the rate of damage to different tagged leaves on the same plant, averaged for the species. I measured the second by an intraclass correlation coefficient, r_I, which estimates the proportion of the total variance in leaf damage attributable to differences in the average damage per plant, where the damage x_{ij} to leaf j on plant i is now measured as ln (1000 times percent damage per day, plus 1). Assuming N leaves in all, distributed over c plants, where plant i has n_i leaves,

$$r_I = \frac{\frac{1}{c-1}\sum_i n_i(\bar{x}_i - \bar{x})^2 - \frac{1}{N-c}\sum_{ij}(x_{ij} - \bar{x}_i)^2}{\frac{1}{c-1}\sum_i n_i(\bar{x}_i - \bar{x})^2 + \frac{1}{c}\sum_{ij}(x_{ij} - \bar{x}_i)^2}$$

where $\bar{x}_i$ is the average damage per leaf on plant i, and $\bar{x}$ is the average damage per leaf for the species as a whole (Snedecor and Cochran, 1967). The interpretation of r_I as the proportion of the variance due to differences between plants assumes that "errors" about the means of different plants are drawn from the same distribution. In the 21 instances where each marked plant had at least two tagged leaves, at least one of which was damaged, I checked this assumption with Bartlett's test for homogeneity of variance (Snedecor and Cochran, 1967).

RESULTS AND DISCUSSION

Leaf Age and Herbivory

Young leaves of both pioneer and persistent species are eaten significantly more than mature leaves (Tables

1 and 2). For persistents this represents a tenfold difference in consumption rates.

Both vertebrate and invertebrate herbivores usually prefer young leaves (Reichle et al., 1973; Kennedy and Booth, 1951; Milton, 1979; Rockwood and Glander, 1979; Feeny, 1970), though there are some exceptions (Claridge and Wilson, 1978; Rhoades, 1977a,b). The higher nitrogen and water contents of young leaves (Dixon, 1970; Milton, 1979; Oelberg, 1956) can increase growth rates of insects (House, 1967; Reese and Beck, 1978; Scriber, 1977; Slansky and Feeny, 1977) and may be one reason for this preference. Some herbivores may prefer young leaves because they are less tough (Grime et al., 1968; Feeny, 1970; Tanton, 1962) and less fibrous (Milton, 1979). Feeny (1976) and Rhoades and Cates (1976) have suggested that young leaves contain lower concentrations of compounds such as tannins which bind with proteins and inhibit digestion, but in three-quarters of the species I studied, tannin concentrations were higher in young leaves (Coley, 1981). Similar results were found for desert shrubs (Rhoades, 1977a,b) and for tropical trees (Milton, 1979). Increased grazing rates on young leaves do not mean that phenolic secondary

Table 1. Wet- and dry-season grazing on young and mature leaves of pioneer and persistent tree species

(continued on next page)

	Persistent species					
	Simarouba amara	*Prioria copaifera*	*Virola sebifera*	*Tetragastris panamensis*	*Trichilia cipo*	*Poulsenia armata*
Wet-season grazing						
Mature leaves:						
Mean (%/day)	0.003	0.002	0.002	0.005	0.003	0.004
Standard deviation	0.010	0.004	0.004	0.013	0.008	0.005
Number of leaves	46	20	31	27	50	25
Coefficients (r_I)	0.32	0.52	0.28	−0.05	−0.01	−0.14
Young leaves:						
Mean (%/day)	0.026	0.014	0.108	1.454	0.522	0.027
Standard deviation	0.066	0.029	0.294	2.435	1.609	0.091
Number of leaves	30	19	24	30	63	33
Coefficients (r_I)	0.18	−0.08+	0.82	0.52	0.01	−0.05
Dry-season grazing						
Mature leaves:						
Mean (%/day)	0.000	0.003	0.003	0.001	0.008	0.007
Standard deviation	0.002	0.015	0.006	0.004	0.064	0.028
Number of leaves	39	30	23	25	131	23
Coefficients (r_I)	−0.04	−0.14	−0.13	−0.01	0.10	−0.02
Young leaves:						
Mean %/day)	1.567	0.581	0.416	0.881	0.606	0.000
Standard deviation	2.352	1.101	1.152	1.617	1.079	—
Number of leaves	32	10	12	34	76	1
Coefficients (r_I)	0.94	0.90	0.60	0.58*	0.92	—
Annual grazing						
Mature leaves (%)	1	1	1	1	2	2

Grazing rates are the percent leaf area eaten per day. An (*) indicates intraclass correlation coefficients (r_I) with inhomogeneous variances ($p<0.05$, Bartlett's test), a (+) indicates no significant difference, and cases where it was not possible to test are unmarked. Species are ranked by annual grazing rates which were extrapolations based on an 8-month wet season. Plant names follow Croat (1978).

Table 1. (continued)

	Persistent species						
	Tachigalia versicolor	*Protium tenuifolium*	*Hirtella triandra*	*Zanthoxylum panamense*	*Quararibea asterolepis*	*Cupania sylvatica*	*Alseis blackiana*
Wet-season grazing							
Mature leaves:							
Mean (%/day)	0.005	0.008	0.042	0.136	0.114	0.311	0.136
Standard deviation	0.014	0.026	0.111	0.632	0.234	1.029	0.480
Number of leaves	36	32	19	49	6	23	15
Coefficients (r_I)	0.23	0.23	0.04	−0.11	0.25+	0.07	0.68
Young leaves:							
Mean (%/day)	0.775	0.928	0.120	0.701	0.316	1.151	0.096
Standard deviation	1.913	2.045	0.201	1.895	0.464	2.588	0.152
Number of leaves	51	54	21	46	16	20	32
Coefficients (r_I)	0.50	0.40	0.60*	0.01	0.72+	0.36+	0.33+
Dry-season grazing							
Mature leaves:							
Mean (%/day)	0.010	0.028	0.019	0.008	0.124	0.026	0.496
Standard deviation	0.019	0.136	0.047	0.026	0.641	0.173	1.327
Number of leaves	35	31	25	42	33	54	27
Coefficients (r_I)	0.13	0.59	−0.01	0.10	0.33	−0.03*	0.13+
Young leaves:							
Mean (%/day)	0.667	1.078	1.278	1.009	0.730	1.786	0.227
Standard deviation	1.332	1.894	2.298	2.048	1.413	2.465	0.634
Number of leaves	66	16	8	20	17	8	11
Coefficients (r_I)	0.52*	0.65	0.37+	0.92	—	1.00	−0.15+
Annual grazing							
Mature leaves (%)	2	5	13	34	43	79	93

compounds are ineffective as grazing deterrents, but simply that they are not sufficient to counter the desirable attributes of young leaves.

The amount of damage tends to vary more among young leaves of a pioneer individual than among its old leaves (Table 3). This implies that young leaves may be less frequently discovered by herbivores, but that when they are, they are eaten more. Leaves are young for only a short period during which they undergo many physical and chemical changes. The time when a herbivore discovers a particular leaf may therefore be critical, because if the leaf is found to be at a palatable stage, it is heavily eaten. The variability between individual pioneer plants (r_I), however, is not significantly greater for young leaves than for old (Table 3). Young pioneer leaves appear to emerge continuously throughout the year, and there are generally a few young leaves of staggered ages on each plant. As a class, young leaves should therefore be as obvious to herbivores as mature leaves.

As with pioneer species, grazing rates on persistents varied more from one young leaf to another than from one mature leaf to another (Table 3). Young leaves are young only briefly, yet they suffer rates of damage an order of magnitude greater than those on mature leaves. Their high palatability and their speed of maturation would both contribute to a high variance in grazing on young leaves. Unlike pioneer spe-

	Pioneer species							
	Zanthoxylum belizense	*Miconia argentea*	*Alchornea costaricensis*	*Spondias radlköferi*	*Luehea seemannii*	*Cecropia insignis*	*Trema micrantha*	*Cecropia obtusifolia*
Wet-season grazing								
Mature leaves:								
Mean (%/day)	0.081	0.189	0.210	0.186	0.456	0.783	1.071	2.267
Standard deviation	0.340	0.354	0.646	0.747	1.255	1.522	1.334	2.584
Number of leaves	24	30	42	88	31	78	30	12
Coefficients (r_l)	−0.06	0.58	0.24+	0.07*	−0.03	0.02	0.17	0.85
Young leaves:								
Mean (%/day)	0.624	0.509	0.818	1.492	1.108	0.111	0.053	1.299
Standard deviation	1.787	1.302	1.760	2.810	1.543	0.466	0.165	1.861
Number of leaves	36	34	44	69	36	68	40	19
Coefficients (r_l)	0.18	0.49	0.15	0.24*	0.22*	0.18	0.14	0.16*
Dry-season grazing								
Mature leaves:								
Mean (%/day)	0.006	0.058	0.026	0.193	0.062	0.019	0.147	1.383
Standard deviation	0.011	0.058	0.055	0.805	0.100	0.061	0.446	1.801
Number of leaves	31	18	14	25	20	41	25	9
Coefficients (r_l)	0.19	−0.02+	0.79	0.16	−0.16+	0.34	0.07	0.74
Young leaves:								
Mean (%/day)	0.038	0.241	2.887	1.687	0.095	0.034	0.330	0.217
Standard deviation	0.129	0.331	2.652	1.801	0.164	0.089	1.187	0.430
Number of leaves	29	14	2	26	3	18	16	13
Coefficients (r_l)	0.59	0.62+	—	0.72	−0.80	−0.22	0.44	0.11+
Annual grazing								
Mature leaves (%)	20	53	54	69	119	193	279	721

cies, persistents have a significantly higher variance between plants for grazing on young leaves (Table 3). All individuals of a persistent species flush young leaves synchronously at the beginning of the rains, perhaps satiating herbivores both locally around individual plants and in the forest at large (Janzen, 1971, 1974; Lloyd and Dybas, 1966; McKey, 1974). The high variation among plants also suggests that grazing damage may be due to specialists, which depend on the chance of finding foliage of a particular species or group of species, or to sedentary generalists (which would cause severe damage on some plants and not on others), rather than mobile generalists (which cannot eat too much of one kind of foliage without risking overdose of some secondary compound).

Plant Life History and Herbivory

Mature leaves of pioneer species are eaten 3–10 times more rapidly than mature leaves of persistent species (Tables 1 and 2). Pioneer species have significantly higher between-leaf variances in damage rates, but the distribution of damage between plants is equally clumped for pioneers and persistents (Table 3).

The lower rates of leaf consumption and the more even rates of damage on mature leaves of persistent species as compared with pioneers (Tables 2 and 3) may reflect features of their growth and dispersal.

Table 2. Grazing rates in relation to season, leaf ages, and life history patterns (% leaf area eaten/day)

Leaf group	*Wet season*				*Dry season*				*Annual rates*[2]
	Mean[1]	*Std. error*	*No. of plants*	*No. of leaves*	*Mean*[1]	*Std. error*	*No. of plants*	*No. of leaves*	
Young pioneer	0.731 a	0.187	91	346	0.521 d	0.368	51	183	
Mature pioneer	0.499 ab	0.167	88	335	0.135 de	0.167	44	121	190.4%
Young persistent	0.539 c	0.134	102	439	0.829 f	0.142	46	311	
Mature persistent	0.048 abc	0.026	105	379	0.043 def	0.038	84	518	21.3%

[1] Values followed by the same letter are significantly different, $p<0.05$ for d and $p<0.01$ for a, b, c, e, and f. Significance levels were determined by a 2-way nested analysis of variance considering leaves as replicates on a transformation of the data: ln (1000 × rate + 1).

[2] Annual rates are the average of the mean rates for each species presented in Table 1.

Table 3. Variability in grazing rates as measured by the variance in damage between plants and between leaves on the same plant

Leaf group	*Leaf variance*[1]		*Plant variance* $(r_I)^2$	
	Wet	*Dry*	*Wet*	*Dry*
1. Young pioneer	6.43	5.53	0.180	0.207
2. Mature pioneer	5.21	2.62	0.230	0.264
3. Young persistent	3.98	3.40	0.366	0.624
4. Mature persistent	1.97	1.78	0.179	0.077
Contrasts[3]				
1 vs. 2	nsd	+	nsd	nsd
3 vs. 4	+ +	+ +	+	+ + +
1 vs. 3	+	nsd	nsd	nsd
2 vs. 4	+ + +	nsd	nsd	nsd

[1] Leaf variances are the between leaf variance in grazing rate for each plant averaged for each species and then for each of the four leaf groups. Calculations were on the transformed data: ln (1000 × rate + 1).

[2] Plant variances are the averages of the intraclass correlation coefficients computed for each species and presented in Table 1.

[3] Contrasts are between leaf groups within seasons. A Mann-Whitney *U* test was used for contrasting 1 vs. 3 and 2 vs. 4, and a paired sign test for contrasting 1 vs. 2 and 3 vs. 4, + $p<0.05$, + + $p<0.025$ and + + + $p<0.005$ (Siegal 1956).

Table 4. Seasonal abundance of young leaves on saplings of 8 pioneer and 13 persistent species

	Number of plants		*Percentage of plants*	
	Dry	*Wet*	*Dry*	*Wet*
Pioneer species				
Old leaves	117	8	32	1
New leaves	250	813	68	99
Persistent species				
Old leaves	339	297	71	33
New leaves	135	601	29	67
Total				
Old leaves	456	305	54	18
New leaves	385	1414	46	82

Values are the number and percentages of plants with mature and young leaves (New) and those with only mature leaves (Old). (All chi-square tests comparing seasonal distribution of new leaves are significant, $p<0.005$).

Persistent species are dispersed throughout the understory and may therefore be easily found by herbivores. They grow slowly and perhaps cannot afford to replace leaves very often, so it is important for them to defend their leaves effectively against herbivores. In my study, persistent species did have higher concentrations of phenolic compounds in the leaves than did pioneers (Coley, 1981). In contrast, pioneer species rely on germination in newly formed light gaps followed by fast growth in order to reach the canopy. They appear to channel their energy into rapid growth rather than expensive defenses. Since pioneer saplings occur only in light gaps, their distribution in the forest is more clumped than saplings of persistent species.

The higher rates of leaf damage sustained by mature leaves of pioneers (Tables 1 and 2) agrees with the prediction that, because they are short lived and fast growing, they need less defense from herbivores than persistents. Damage varies from one mature leaf to another in pioneers (Table 3) as if these leaves were primarily eaten by specialist herbivores which, once on a leaf, stay and devour large portions of it, unembarrassed by the secondary compounds it contains. In contrast, the low variance between mature leaves of persistents (Table 3) suggests damage by more mobile generalist herbivores which feed for one time and then leave the leaf, perhaps to avoid risking an overdose of some secondary compound. This is in accord with extrapolations from current theories of interactions between plants and herbivores (Feeny, 1976; Rhoades and Cates, 1976). These theories also predict that pioneers are less "apparent" to herbivores, primarily escaping discovery because they occur in clumps, only in gaps. This does not seem to be true, since the r_I estimate of the proportion of variability attributed to between plant differences is not significantly different between pioneer and persistents (Table 3).

Young leaves of pioneers and persistents are eaten at the same relatively high rates (Tables 1 and 2), but the distribution of damage among leaves and among plants differs. Pioneers have a high variance between leaves on the same plant (Table 3). This may be because the average time a given leaf remains young is shorter for pioneers (38 days) than for persistents (56 days), and because there are several young leaves of staggered ages on pioneer plants at one time. Only some of these young leaves, however, will be an appropriate food resource for a herbivore. Since persistent plants produce a flush of young leaves all of the same age, they are equally palatable and have the same chance of being eaten. This would also cause the major source of variation to be between plants and not between leaves on the same plant. A higher intraclass correlation coefficient for young persistent leaves, though not quite significant, supports this (Table 3).

Seasonal Variation: Grazing on Mature Leaves

Grazing on mature leaves is greater in the wet season for just over half of the species studied (Table 1). Averaging over all species, grazing on mature leaves is 2.3 times higher in the wet season with the differences being most marked for pioneers ($p < 0.025$, paired t-test for species averages of herbivory on mature leaves). Insect abundance and activity are probably the main factors responsible for the elevated levels of herbivory in the early wet season (Smythe, this volume; Wolda, 1978).

Seasonal Variation: Grazing on Young Leaves

Almost twice as many plants in the light gaps I studied had young leaves in the wet season as in the dry season (Table 4). For both pioneer and persistent species these differences in the seasonal distribution of young leaves was significant (chi-square, $p < 0.005$). The differences for persistent species are more dramatic, with most plants waiting until the rains to put out a flush of new leaves. A similar rhythm of leaf production is found in canopy trees on Barro Colorado Island (Leigh and Smythe, 1978).

The amount and distribution of grazing damage on young pioneer leaves shows little seasonal variation (Table 2 and 3). Though there are fewer plants with young leaves in the dry season (Table 4), the difference is not as dramatic as with persistents, and the reduction in the number of young leaves may be balanced by the reduction in herbivores (Smythe, this volume; Wolda, 1978).

Patterns of grazing on young persistent leaves are quite different than on the other leaf groups. They are the only group that has higher rates of herbivore damage (Table 2) in the dry season and fewer leaves with no damage. The variability between leaves on a plant does not change seasonally, but the variability between plants is slightly higher in the dry season. The seasonal distribution of young persistent leaves (Table 4) may have a strong influence on the vulnerability of those leaves to herbivores. The synchronous emergence of young leaves at the beginning of the rains is probably effective in satiating herbivores and causes the lower rates of damage. Clumping of damage among plants (r_I, Table 3) is higher in the dry season, perhaps because of reduced movements of herbivores and increased grazing pressure on the young leaves that are present.

Annual Rates of Herbivory

I obtained estimates of the annual loss of leaf area by extrapolating from the grazing rates on mature leaves measured in this study (Tables 1 and 2). I averaged rates of leaf consumption for all my study species, but because species were not sampled in proportion to their abundance, this may not provide an accurate measure of herbivory in the forest as a whole. Herbivore pressure may also be quite different in the canopy. The annual rates would be higher if damage to young leaves were included, but I cannot measure this damage because I do not know how long leaves of different species remain young. Because these data were collected in order to determine loss of functional leaf area to the plant, they include necrotic areas and are not necessarily the amount of leaf area passing to herbivores.

The annual rate of leaf loss for mature leaves of persistent species is 21% of the leaf area (Table 2). This is high, but within the range of estimates for other forests: 20–60% for eucalyptus forests (Burden and Chilvers, 1974; Fox and Macauley, 1977; Misra, 1968; Springett, 1978), 5–10% for temperate forests (Bray, 1964, Fünke, 1973; Kaczmarek, 1967; Nielsen, 1978; Reichle and Crossley, 1967; Reichle et al., 1973; Woodwell and Whittaker, 1968) and 7–9% for tropical forests (Leigh and Smythe, 1978; Odum and Ruiz-Reyes, 1970). The average annual rate for mature leaves from pioneers is 190%. This estimate seems large, but fits with the observation that many pioneer saplings keep an individual leaf for only a few months. Leaf life on adult trees may be much longer.

There are several possible reasons why I found higher annual rates of herbivory than other researchers. They judged grazing from holes in either fallen leaves or in live leaves at the end of the growing season. I included necrotic areas in damage estimates which might not be noticeable on a dried fallen leaf. In addition, these measures of standing crop ignore leaves that were totally eaten, had been chewed off at the petiole, or had been dropped due to excessive blade damage. These forms of damage contribute significantly to a plant's loss of leaves. Of the 1353 mature leaves that were marked and measured in this study, 36 or 2.7% were completely eaten. This small percentage of wholly eaten leaves contributes substantially to the average grazing rates. Removing these leaves from the analysis, the annual rate becomes 13.2% for persistents and 116.3% for pioneers. The contributions of wholly eaten leaves to the annual rate of leaf loss is approximately 38%. Previous studies of herbivory may therefore considerably underestimate both the amount of damaged leaf area and the amount of tissue passing to herbivores.

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