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CAN APPARENT LEAF DAMAGE IN TROPICAL TREES BE PREDICTED BY HERBIVORE LOAD OR HOST-RELATED VARIABLES? A CASE STUDY IN PAPUA NEW GUINEA

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ABSTRACT. Local patterns of leaf damage for ten tree species of different plant families and of different successional status were examined at Wau, Papua New Guinea. Damage to mature leaves was expressed as apparent percentage area lost in leaf samples (ALD, apparent leaf damage, visual estimations), area removed per leaf (ARL) and biomass removed per leaf (BRL). Leaf damage varied greatly among species, from 3.8 to 19.7% for ALD, from 5.7 to 28.9 cm^2 for ARL, and from 0.05 to 0.50 g dry weight of BRL. However, leaf damage was difficult to predict from either insect-related variables (species richness, abundance, biomass and specialization of associated herbivores; enemy-free space) or host-related variables (taxonomic relatedness, tree architecture, water and nitrogen content of leaves, etc.). In particular, trees with species-rich herbivore faunas or with high herbivore densities were not always likely to experience high damage. Contrary to expectations, leaf palatability, successional status or leaf production patterns did not clearly influence leaf damage. The skewness of damage distribution appeared to be weakly correlated with leaf size. This observation was tentatively interpreted as the result of a particular adaptive foraging and feeding behaviour of insect herbivores on large-leaved trees in order to escape avian predators. We conclude that leaf damage is likely to depend on the feeding behavior of a few dominant leaf-chewing insect species and this may complicate the interpretation of results obtained in studies of herbivory seeking community-level patterns. These results point out that the biological interpretation of measurements of apparent leaf damage may not be straightforward.

INTRODUCTION

Elton (1973) summed up observations about invertebrate communities of two rain forests, in Panama and Brazil. His temperate experience provided him the opportunity to contrast species richness, abundance, body size, and the abundance of predators in tropical and temperate forests. Some of his observations had been intuitively known or expected by tropical ecologists. For example, Elton reported an apparent scarcity of insect herbivores in the two rain forests he studied, particularly in the shrub layer and during day-time. Despite this, he was surprised to observe that levels of leaf damage in these forests were relatively high compared to these in temperate forests.

More recently, Lowman (1984), and Coley and Aide (1991) showed that reported annual rates of herbivory in tropical forests (10.9% of leaf area removed on average) are higher than in temperate forests (7.5%). Coley and Aide (1991) argued that higher herbivory in the tropics could result from either greater herbivore loads (measured either in terms of species number, individual numbers (density) or biomass) or lower levels of defences and further showed that the latter was unlikely, since tropical plants are usually better defended than temperate ones. As to herbivore loads, the meager existing evidence suggests that at least herbivore density measured at one point in time is lower in tropical than in temperate forests (Basset *et al.* 1992; Y. Basset, unpubl. data). Thus, Elton's (1973) observations provide an apparent paradox which has not been resolved yet (e.g., Greenwood 1991, Basset *et al.* 1992).

Elton (1973) attempted to explain his observations by suggesting that insect herbivores are highly active during night-time but difficult to observe during day-time. One study of arthropod diel activity patterns in Papua New Guinea (Springate & Basset in press) showed that this was unlikely to be a general explanation. Elton (1973) did not attempt to quantify leaf damage but based his impression on discrete and visual assessments (i.e., leaves are selected at one point in time), a practice common in many short-term studies (e.g., Wint 1983).

Discrete estimates of leaf damage are often assessed visually and referred to as percentage of "apparent leaf damage" (ALD; see Lowman 1985). In contrast, long-term assessment of grazing rates refer to the amount of leaf tissue removed during a certain period, sometimes the lifetime of the leaves (Lowman 1984). ALD may

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result from at least four different factors: (a) actual damage by herbivores, often during leaf expansion; (b) necrosis of leaf tissue resulting from fungi and microbes; (c) mechanical damage due to rainfall and falling debris; and (d) subsequent hole expansion during leaf growth (Lowman 1984; Landsberg 1989). The latter may be of particular significance in rain forests since insect damage is often concentrated on young leaves (e.g., Coley 1983; Lowman 1985). There is usually a good correlation between estimates of ALD and grazing rates (e.g., Lowman 1984: Table 1: Spearman's rank correlation coefficient $r_s = 0.692$, $p < 0.01$) but the former usually underestimates actual damage, often by a factor of 2.5, because leaves entirely eaten are rarely accounted for (Lowman 1984).

As part of a study investigating the species richness and host specificity of leaf-chewing insects associated with ten species of forest trees in Papua New Guinea (Y. Basset, unpubl. data), apparent leaf damage was measured. This paper investigates whether local patterns of leaf damage on the mature leaves of each species can be predicted from either insect-related variables (i.e., species richness, density and biomass of associated herbivores; densities of ants and other enemies) or host-related variables (i.e., simple measurements of plant architecture and biochemistry). The findings are discussed in the light of Elton's (1973) paradox, and addresses the relative scarcity of insect herbivores in rain forests and their apparent high damage to vegetation.

MATERIAL AND METHODS

Study Area and Study Plants

The study was performed on the slopes of Mt. Kaindi, near and within the grounds of the Wau Ecology Institute, Wau, Papua New Guinea (7°24'S, 146°44'E). Altitude of collecting ranged from 1100–2362 m (summit), but most work was done between 1200—1400 m. Mt. Kaindi has been partially cleared, leaving a mosaic of grasslands and forest patches, dominated by secondary forest (Van Valkenburg & Ketner 1994). The main forest formations encountered on the slopes include lower and mid-montane rain forest (Johns 1982). The climate is classified as "humid to perhumid mesothermal with little or no water deficit" (McAlpine *et al.* 1983). The study area is further detailed by Gressitt and Nadkarni (1978), and Van Valkenburg and Ketner (1994).

Ten woody plant species (native forest trees and shrubs) were studied (Table 1). They were chosen as representative of different plant families and included both pioneer and persistent species. Hereafter, the host plants are designated by their generic names.

Assessment of Herbivore Species Richness and Specialization

Leaf-chewing insects feeding externally (most Lepidoptera larvae, some adults and larvae of the Curculionidae, Chrysomelidae and other beetles, some larvae and adults of the Orthoptera and Phasmatodea) were collected exclusively from the foliage of the study trees during day- and night-time by hand collecting, foliage beating and branch clipping (see below for description of the latter procedure). Sampling was performed almost daily from February to July 1992 and from November 1992 to April 1993 (during occasional short wetter and drier periods). When the foliage could not be sampled from the ground, the single rope technique provided access to the crowns (Perry 1978). Sampling effort was the same for each tree species (300 beating samples, about 33 m^2 of foliage clipped and 50 hours of observation). Between 3 to 41 individual trees were sampled for each tree species, depending on local tree abundance and size.

Insect specialization was assessed from feeding trials in the laboratory. Live insects were stored in plastic vials, at room temperature and high relative humidity. Insects were provided with fresh foliage of the tree species from which they were collected, until they died or accepted food. In the latter case only, identification numbers corresponding to morphospecies (hereafter termed species) were assigned to the insects. Thus, the protocol excluded "incidental" herbivores (resting but not feeding on the foliage) from the analyses. Species assignment was later checked by taxonomists at the Bishop Museum, Honolulu.

Insects were then tested in random order for 24 h periods on the foliage of the nine other study species. Feeding damage was scored visually, relative to insect body size, on a logarithmic scale, as follows: 0: no feeding; 1: attempting to feed; 10: moderate feeding; 100: extensive feeding. This procedure emphasized regular feeding as compared to food-probing. Insects were assigned to three categories according to the results of these feeding tests: (a) "specialists", insects tested on three or more plant species but which only fed on the plant they were collected from (sum of feeding scores < 100); (b) "generalists", insects tested on three or more plant species and which fed on two or more plants, belonging to different plant families (sum of feeding scores >= 100); and (c) "uncertains", insects which, because of death or pupation, could not be tested on more

TABLE 1. Study trees and shrubs (*); their successional status (Pi = pioneer, Pe = persistent); mean (SE) apparent leaf damage (ALD); mean (SE) area removed per leaf (ARL); mean (SE) biomass removed per leaf (BRL); index of leaf palatability (number of morphospecies tested, see text) and phenology of leaf production. Species are evergreen unless indicated.

Hosts	Plant family	Status	ALD (%)	ARL (cm^2)	BRL (g DW)	Palatability (score)	Leaf production
Elmerrillia tsiampacca (L.) Dandy	Magnoliaceae	Pe	3.8 (0.41)	9.6 (1.0)	0.09 (0.01)	22.13 (247)	Continuous
Cinnamomum cf. *culilaban* (L.) Presl	Lauraceae	Pe	18.1 (1.12)	16.7 (1.0)	0.20 (0.01)	15.94 (247)	Intermittent leaf flushes[1]
Piper plagiophyllum K. Sch. & Laut.*	Piperaceae	Pi	10.4 (0.87)	19.9 (1.7)	0.12 (0.01)	6.52 (242)	Continuous
Ficus nodosa Teys. & Binn.	Moraceae	Pi	6.5 (0.85)	27.2 (3.6)	0.27 (0.04)	40.55 (243)	Deciduous, leaf flushes[1]
Pipturus argenteus Wedd.*	Urticaceae	Pi	19.7 (1.28)	23.7 (1.6)	0.15 (0.01)	12.14 (246)	Continuous
Castanopsis acuminatissima A. DC.	Fagaceae	Pe	12.6 (1.11)	5.7 (0.5)	0.08 (0.01)	19.97 (243)	Intermittent leaf flushes[1]
Caldcluvia brassii Hoogl.	Cunioniaceae	Pi	16.7 (1.36)	28.9 (2.4)	0.50 (0.04)	21.77 (247)	Continuous
Aleurites moluccana Willd.	Euphorbiaceae	Pe	4.9 (0.61)	11.5 (1.5)	0.08 (0.01)	31.32 (246)	Continuous
Melicope denhamii (Seem.) T. Hartley	Rutaceae	Pe	7.7 (0.89)	9.8 (1.1)	0.10 (0.01)	15.49 (243)	Intermittent leaf flushes[1]
Cordia dichotoma Forst.	Boraginaceae	Pi	18.0 (1.12)	14.9 (0.9)	0.05 (0.003)	26.86 (244)	Deciduous, leaf flushes[1]

[1] Apparently 2–3 times a year, as a synchronous event.

than two plant species. The procedure is further discussed in Basset (1994).

An index of leaf palatability for leaf-chewing insects was calculated by summing damage scores of all species tested on a particular tree species divided by the number of species tested on this tree species. Index values range theoretically from 0 to 100 (high scores denote a high palatability) and allow comparison among plant species. Since insects were tested but not scored on the hosts from which they were collected, palatability scores are independent of the number of insect species collected from the tree species considered.

The biomass of an individual of each insect species was estimated using the regressions between body length and insect biomass (g dry weight) computed by Schoener (1980; regressions for tropical rainforest insects were used). A mean of 10 measurements was used for adult specimens. For caterpillars, the highest measurement recorded was used for each species, as an estimate of the body length of the last instar.

Assessment of Herbivore Density, Biomass, and Leaf Damage

For each tree species, a total of 55 branch clipping samples were obtained from 11 individual trees (3 individuals in the case of *Cordia*), at different times of the year, both during day- (40 samples) and night-time (15 samples), as follows. Each sample consisted of a few branches (1–5) which were enclosed in a large heavy duty plastic bag; the branches were clipped off and the contents of the bag were examined in the laboratory. Herbivores were counted and the leaves of the sample were oven-dried for 24 h at 100°C. Previously established highly-significant regressions between leaf weight and leaf size for each tree species (Y. Basset, unpubl. data) were used to compute the total leaf area of the sample. Since sample size varied little among individual trees and species (Y. Basset, unpubl. data), catches were not corrected according to sample size. From these measurements and from the whole of the sampling program, the following insect-related variables were derived for each tree species: number of species of chewers, specialist chewers, generalist chewers, and lepidopteran species. For each sample (each representing on average 0.6 m^2 of leaf area), we calculated the mean number and dry mass (mg) for chewing insects and caterpillars, plus the mean number of enemies (including arthropod and insect predators, ants, and insect parasitoids).

For each tree species on 11 sampling occasions, leaves were collected in sealed plastic bags. Twenty leaf discs of 0.28 cm^2 were randomly punched from each sample and weighed, within 2–3 h of collection. The discs were dried for 24 h at 100°C and specific leaf weight (g dry weight $\times$ cm^{-2} fresh area) and leaf water content (% fresh weight) were calculated.

Waller and Jones (1989) showed that interspecific differences in leaf densities influence measurements of leaf damage and their interpretation. Because leaf size and leaf density varied considerably among tree species, three related measurements of leaf damage were considered, all obtained from branch clipping samples. First, ALD was estimated visually and expressed as % of leaf area missing. For each sample, 15 mature leaves were randomly chosen and scored according to the standard procedure developed by Wint (1983). Thus, a mean of 825 leaves were scored for each tree species. Leaves were scored in the following classes: 0: 0%, 1: 1%, 2: 2–5%, 3: 5–10%, 4: 10–20%, 5: 20–50%, 6: 50–80% and 7: 80–100% (Wint 1983). The average ALD of the sample was calculated as the average percentage damage per leaf, obtained by summing the mid-point value of corresponding class scores and dividing this sum by the number of leaves (Wint 1983). Leaf-miner tracks were not included in this assessment of chewing damage.

Second, a crude estimate of area removed per leaf (ARL) was calculated as follows:

$$\text{ARL } (\text{cm}^2) = \text{ALD}/100 \times \text{mean leaf size (double-sided area, cm}^2)$$

Third, a similar estimate of biomass removed per leaf (BRL) was calculated as:

$$\text{BRL (g dry weight)} = \text{ALD}/100 \times \text{mean leaf size } (\text{cm}^2) \times \text{mean specific leaf weight (g dry weight} \times \text{cm}^{-2})$$

All measurements can be readily compared among tree species. We reasoned that some of these measurements may be important from an entomocentric point of view (i.e. more easily predicted by insect variables), while others may be important from a phytocentric perspective (i.e. more easily predicted by plant variables).

Measurement of Plant Variables

Several plant-related attributes which could potentially influence leaf damage were considered for each study tree. The variables included: (1) historical variable: taxonomic relatedness of the host; (2) variables related to growth dynamics (growth patterns, proportion of new leaves, duration of leaf expansion, flushing synchrony); (3) variables related to growth strategy (successional status and local abundance); (4) architecture (tree height, leaf size, leaf weight (related to leaf toughness) and leaf pubescence; and (5) simple aspects

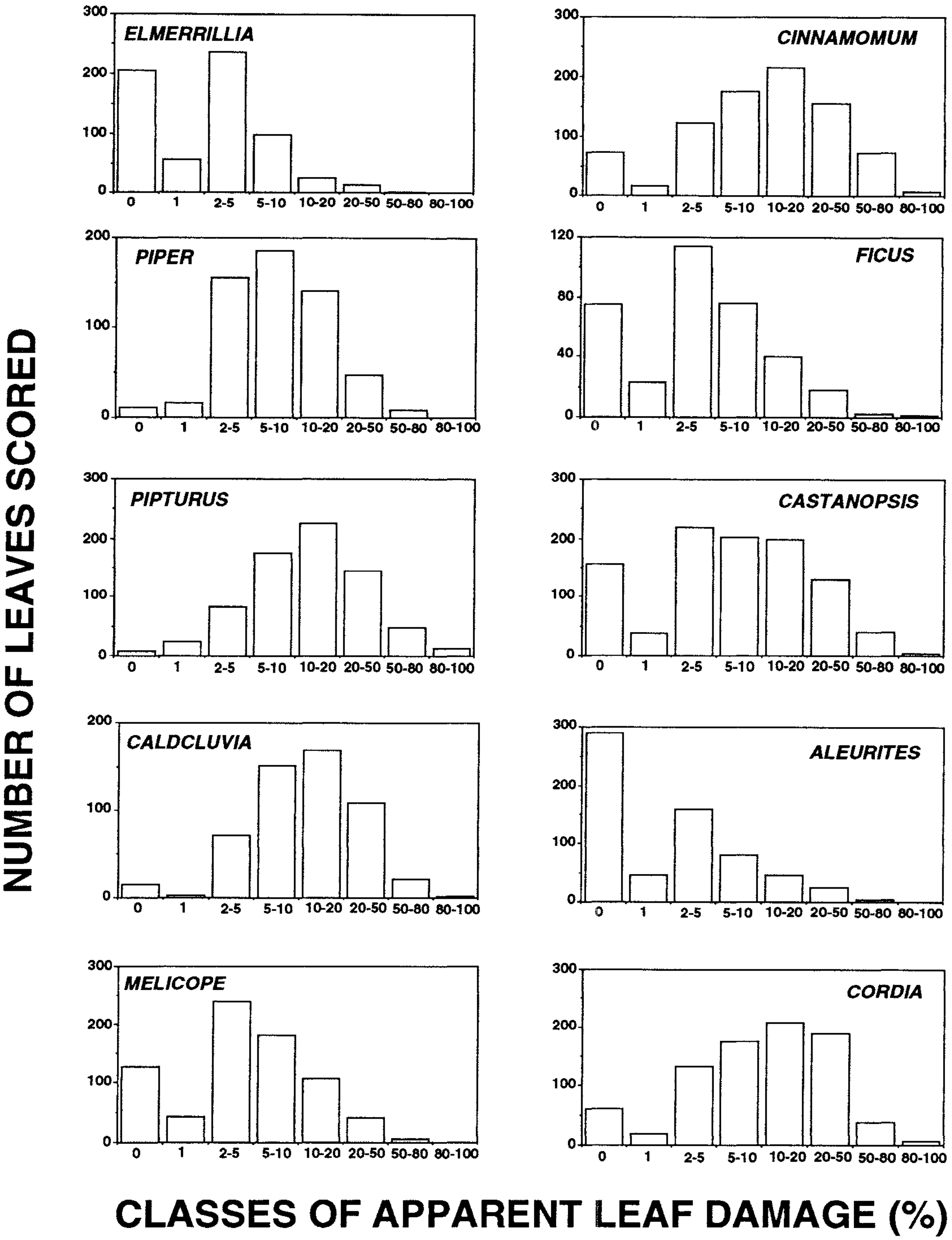

FIGURE 1. Frequency distribution of damage per scoring class of apparent leaf damage, detailed for each tree species studied.

TABLE 2. Summary statistics of the frequency distribution of apparent leaf damage (ALD) for each of the tree species studied (no. of leaves censused, coefficient of variation, skewness, kurtosis and G-test of independence with overall distribution when leaves of all tree species were pooled).

Tree	No. leaves	CV	Skewness	Kurtosis	G-test
Elmerrillia	637	1.806	4.652	29.160	357.3***
Cinnamomum	840	1.046	1.440	1.423	132.8***
Piper	564	1.027	2.397	7.227	123.0***
Ficus	349	1.548	3.593	18.158	73.9***
Pipturus	722	0.961	1.666	2.584	276.5***
Castanopsis	991	1.267	2.007	4.163	2.31 n.s.
Caldcluvia	542	0.892	1.704	3.220	148.1***
Aleurites	651	1.998	3.594	15.775	407.3***
Melicope	746	1.347	2.797	10.030	107.9***
Cordia	831	1.001	1.520	2.415	117.7***

*** $P < 0.001$.

of plant chemistry (water content, total foliar nitrogen and potassium of mature leaves and leaf palatability for leaf-chewing insects).

Most of the important variables are further explained and presented in Table 1 and in Appendix 1. Insect variables and a full account of host variables will be discussed elsewhere (Y. Basset, unpubl. data). Since leaf damage is typically distributed non-normally (Landsberg 1989), we used non-parametric statistics to test possible differences and correlations between variables. We used the Bonferroni sequential technique when performing several simultaneous correlations, to reduce the probability of making type-I errors (Rice 1989).

RESULTS

Overall Levels of Leaf Damage and Interspecific Differences

When data were pooled for the ten tree species studied, mean ALD amounted to 12.0 ± 0.4% per sample, mean ARL to 16.3 ± 0.6 cm^2 per leaf and mean BRL to 0.16 ± 0.01 g dry weight per leaf. ARL and BRL were positively correlated ($r_s = 0.790$, $p < 0.05$), whereas there was no significant correlation between ALD and ARL or BRL ($r_s = 0.382$, $p > 0.20$; $r_s = 0.225$, $p > 0.50$, respectively). The frequency distribution of ALD is shown for each tree species in Fig. 1.

Apparent leaf damage (Kruskall-Wallis $W = 247.4$, $p < 0.001$), ARL ($W = 195.8$, $p < 0.001$) and BRL ($W = 239.6$, $p < 0.001$) differed significantly among tree species. Average leaf damage varied greatly among species and depending on which measurement of leaf damage was used, species showing low and high levels of damage were different (Table 1).

When the frequency distribution of leaf damage was examined for each tree species (Table 2), most distributions were different from each other (Fig. 1) and, in particular, from the overall distribution, with the exception of *Castanopsis* (Table 2). All distributions were positively skewed, but to various degrees (*Elmerrillia*, *Aleurites*, *Ficus* highly skewed; *Cinnamomum*, *Cordia* less so). Interestingly, there was a negative correlation between ALD and both skewness ($r_s = -0.964$, $p < 0.001$) and coefficient of variation ($r_s = -0.842$, $p < 0.01$).

Leaf Damage in Relation to Insect Variables

There were no significant correlation between the different measurements of leaf damage and the different variables accounting for the species richness of associated herbivores (Table 3). There was a weak trend for ALD to be positively correlated with the biomass of chewers within clipping samples. However, this relationship, as others, was not significant when examined with the Bonferroni sequential technique. Densities of enemies and, in particular, of ants ($r_s = 0.503$, $p = 0.86$), were not clearly related to leaf damage.

Leaf Damage in Relation to Host Variables

Leaf damage was also difficult to predict from host-related variables (Table 3). Two weak relationships were detected: (1) ALD was negatively correlated with leaf size (Table 3); and (2) the skewness of damage distribution (ALD) was positively correlated with leaf size ($r_s = 0.782$, $p < 0.05$). However, neither of these relationships was significant when examined with the Bonferroni sequential technique. None of the variables relating to leaf damage was clearly correlated with leaf palatability, synchrony of leaf production, leaf expansion rates, leaf nitrogen or taxonomic relatedness. Successional status influenced leaf damage expressed as loss of area per leaf only: pioneer trees were more likely to suffer high damage than persistent trees (Table 4). Leaf produc-

TABLE 3. Spearman's rank correlation coefficients for leaf damage and (a) insect-related variables [number of species of chewers (SP), number of species of specialist chewers (SPS), number of species of generalist chewers (SPG), number of lepidopteran species (SPL), density of chewers (DCH), biomass of chewers (BCH), density of caterpillars (DCA), biomass of caterpillars (BCA) and densities of enemies (ENN)]; and (b) host-related variables [taxonomic relatedness (TAXO), number of young leaves in branch-clipping samples (NOYL), leaf expansion (EXPA), local tree abundance (ABUN), tree height (HEIG), leaf size (SIZE), water content (LWC) and nitrogen content (NITR) of mature leaves, and leaf palatability (PAL)].

a) Insect-related variables

	SP	SPS	SPG	SPL	DCH	BCH	DCA	BCA	ENN
ALD	0.442	0.503	0.323	0.353	0.709*	0.733*	0.612	0.657*	0.584
ARL	0.152	0.091	0.348	−0.128	0.248	0.176	0.018	0.079	−0.237
BRL	0.097	0.097	0.202	−0.122	0.006	0.170	−0.164	−0.113	−0.189

b) Host-related variables

	TAXO	NOYL	EXPA	ABUN	HEIG	SIZE	LWC	NITR	PAL
ALD	0.122	0.661*	0.164	0.458	−0.600	−0.745*	−0.042	0.018	−0.467
ARL	0.555	0.152	0.176	−0.025	−0.661*	0.273	0.079	−0.006	−0.018
BRL	0.593	0.328	0.426	0.319	−0.517	0.328	−0.377	−0.401	−0.176

* $P < 0.05$. However, none of the correlations are significant when using the Bonferroni sequential technique, with the corrected probability level of $\alpha = 0.05/18 = 0.0027$ (18 simultaneous tests performed for each leaf damage variable).

tion did not influence patterns of leaf damage and the skewness of distribution of leaf damage was unaffected by the different grouping variables (Table 4).

DISCUSSION

Expressing leaf damage as different variables did not improve our biological interpretations. Damage expressed as percentage of leaf area lost was often involved in some weak correlations with insect- and host-related variables and seemed therefore to be the most appropriate variable to use.

Although we measured many variables hypothesized in other studies to explain patterns of leaf damage, none was strongly correlated with any measurement of leaf damage. In particular, our analyses emphasized the poor (or absence of) correlations between leaf damage and insect variables. This is perhaps surprising and deserves further attention, because apparent leaf damage is often assumed to be related to insect species richness, abundance or biomass on their hosts (e.g., Coley 1983, discussing spatial distribution of herbivory). In our study, the different measurements of leaf damage were neither correlated with the species richness of all associated herbivores, of specialist herbivores, or of caterpillar species. This concurs with the results of Marquis (1991) who examined leaf damage and herbivore species richness on several species of *Piper* in Costa Rica and found little correspondence between the two variables. Patterns in leaf damage are more likely to depend on the feeding behavior of a few dominant herbivore species and the time the damage was caused than on herbivore load expressed as species richness. For example, on *Piper* (although the herbivore fauna was rather species-poor), it did not prevent voracious feeders such as *Milionia* sp., a geometrid specialist, from causing relatively high damage. Conversely, on *Ficus*, Chrysomelidae were well diversified but these small insects never attained densities which created extensive damage (Y. Basset, pers. obs.). Similar arguments can probably explain

TABLE 4. Test for possible differences (Mann-Whitney *U*) in leaf damage and skewness of distribution of leaf damage between trees of different successional status, different leaf production strategies and different local abundances.

Grouping variable	ALD	ARL	BRL	Skewness
Successional status[1]	18.00, $P = 0.251$	24.00, $P = 0.016$	18.00, $P = 0.249$	8.00, $P = 0.347$
Leaf production[2]	10.00, $P = 0.602$	16.00, $P = 0.465$	14.50, $P = 0.675$	17.00, $P = 0.347$
Local abundance[3]	4.00, $P = 0.076$	12.00, $P = 0.917$	7.50, $P = 0.295$	20.00, $P = 0.117$

[1] Pioneer or persistent species, see Table 1.

[2] Continuous production throughout the year or distinct leaf flushes, see Table 1.

[3] Less common, ranked 1 or 2; more common, ranked 3 or 4, see Appendix.

the lack of a strong relationship between herbivore abundance and biomass and leaf damage at the community level (i.e., when the 10 tree species were considered together).

Enemy-free space, as measured by the density of ants, spiders, insect predators, and parasitoids, did not appear consistently to influence patterns of leaf damage when considered at the community level. This concurs with results of several studies, in the Neotropics and in the Old World tropics (e.g., Whalen & Mackay 1988, Fiala *et al.* 1989, Fowler 1993).

Coley (1983) investigated the grazing rates on 46 species of saplings on Barro Colorado Island, but did not provide any information about herbivore loads on the different hosts studied. In her study, over 70% of the variance in grazing rates on mature leaves could be explained primarily by leaf toughness, water and fiber contents, and secondarily by leaf protein and phenolics. Leaf expansion times and flushing synchrony did not appear to influence grazing rates in Coley's study, as in our case and in another community study on Barro Colorado Island (Aide 1993). Although we measured most of the variables that Coley used in her analysis with similar methods, we could not explain leaf damage to the extent she did. This discrepancy may be due to either or both of the following factors: (1) differences in methodology: discrete estimates versus grazing rates and much lower sample size in our case. In particular, interspecific differences in discrete measurements of leaf damage may be influenced by non-herbivore factors. (2) Different herbivore species or communities resulting in different patterns of damage (e.g., different feeding behaviors; different ratio of specialists to generalists, etc.). (3) Coley used understorey leaves only on saplings, which are renown for relatively high herbivory as compared to tall trees (Lowman 1985, 1992). It is not known whether insect foraging and feeding behaviors on saplings are similar to those on mature trees.

The strongest correlations that we established were between ALD and the skewness of damage distribution (a negative correlation); and between leaf size and both ALD and skewness of damage (negative and positive correlations, respectively): trees with large leaves were less likely to experience high damage levels overall and on these trees, the distribution of damage was highly positively skewed. We believe that this may result from the foraging and feeding behavior of insect herbivores, which may be particularly conspicuous to their enemies when on trees with large leaves. In this instance, it may be advantageous for the herbivore to proceed by isolated feeding bouts, distant from each other, in which a high quantity of foliage is ingested, in order to spread leaf damage and to escape from visually-oriented predators, such as birds (Heinrich & Collins 1983). Thus, in the system under study, the best predictor (leaf size) appeared to be related to a probable result of herbivore behavior (skewness of damage distribution). However, this interpretation should be viewed with caution, since the Bonferroni technique suggested that the correlations obtained may be due to chance only. Studies encompassing larger sample sizes (i.e., number of tree species investigated) are urgently and absolutely needed to elucidate this point.

Would Elton's (1973) conclusions have been different if he had measured leaf damage using grazing rates instead of discrete estimates? This point is not trivial and deserves more attention (Lowman 1984, Coley & Aide 1991). However, and perhaps equally crucial, the correct interpretation of Elton's paradox relies also on a correct estimation of herbivore loads. The impact of herbivores on their hosts may depend on species richness, density and biomass of herbivores, but also on their particular foraging and feeding behaviors, particularly of the dominant species. Owen (1983) discussed the difficulty of obtaining reliable estimates of animal abundance in rain forests. He pointed out that many tropical species of butterflies are abundant as caterpillar or adult for very short periods, whereas their leaf damage remains conspicuous for long periods. When averaged throughout the whole year, herbivore loads in the tropics may not be particularly lower than that in temperate woodlands (Owen 1983). Our data suggested that, as far as leaf damage is concerned, the impact of herbivores is difficult to express in terms of species richness, density and biomass, presumably because of the particular feeding behavior of the dominant herbivore species, which may mask other patterns. If our results can be validated more generally, then Elton's observations would not appear so conflicting. The next question to ask is why particular insect species consume more foliage in the tropics than their counterparts in temperate regions. For example, tropical herbivores may compensate for the poor nutrient quality of rainforest leaves by high grazing rates (e.g., Moore & Francis 1991).

If the conclusions of our study are not confounded by methodological problems, we see that leaf damage is likely to result mainly from the feeding behavior of a few dominant leaf-chewing species. Similarly, Bernays and Graham (1988) argued that the major impact of insect herbivores on plants comes from relatively few species, because most of them are usually rare. While these considerations may be relatively insignificant when studying the impact of herbivory on plant fitness (i.e., the phytocentric perspective), this may complicate the interpretation of results seeking patterns of herbivore distribution on host-plants (i.e., the entomocentric perspective). For example, in our case, leaf palatability, as measured for the local insect community, was not correlated with leaf damage, a rather different conclusion from that of Coley (1983). If anything, the different points raised in this discussion emphasize that the biological interpretation of apparent leaf damage, particularly as a substitute for insect-related variables, may not be straightforward.

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APPENDIX 1. Insect- and host-related variables[1] determined for each tree species studied. Coding variables as indicated in Table 3. Mean densities and biomass of insects are expressed per 0.6 m^2 of leaf area.

Tree species	SP	SPS	SPG	SPL	DCH	BCH	DCA	BCA	ENN	TAXO	NOYL	EXPA	ABUN	HEIG	SIZE	LWC	NITR
Elmerrillia	20	4	7	12	0.42	1.09	0.38	0.97	2.91	2	66	29.6	2	19.4	251.8	61.6	1.69
Cinnamomum	37	16	17	29	1.53	5.74	1.36	3.25	7.58	21	345	35.5	3	7.0	92.0	49.0	1.31
Piper	18	6	10	10	1.09	2.51	0.35	1.14	5.16	100	108	20.7	2	4.5	192.3	74.3	3.68
Ficus	61	36	21	38	1.69	3.96	0.71	1.98	5.45	138	408	24.2	2	16.3	417.1	61.6	1.78
Pipturus	52	24	16	21	3.20	12.85	1.40	4.97	7.84	12	681	32.5	4	4.2	121.6	65.0	2.68
Castanopsis	94	53	20	83	3.13	8.44	2.95	7.49	14.22	1	1068	26.5	4	17.2	45.0	49.1	1.60
Caldcluvia	39	11	25	18	1.07	7.96	0.55	1.32	1.73	5	623	70.0	3	3.4	173.3	53.0	1.17
Aleurites	25	3	16	15	0.55	1.39	0.44	1.32	2.53	1	87	34.9	2	16.3	237.5	63.9	2.24
Melicope	36	13	20	24	0.47	7.74	0.24	0.70	5.45	37	356	26.2	3	6.1	127.7	61.5	2.26
Cordia	45	19	23	38	2.31	5.80	1.84	4.50	5.60	5	394	19.8	1	12.7	82.6	71.8	3.42

[1] Host-related variables: TAXO = taxonomic relatedness: number of congeneric plant-species as reported in the New Guinean checklist of Höft (1992); NOYL = number of newly emerged leaves/leaflets as recorded in branch-clipping samples; EXPA = leaf expansion: mean number of days from bud burst to leaf maturation as measured on tagged leaves; ABUN = local tree abundance, ranked from 1 to 4; HEIG = mean tree height (m); SIZE = mean leaf/leaflet size (cm^2); LWC = mean water content of mature leaves (% fresh weight); and NITR = mean nitrogen content of mature leaves (% dry weight, Kjeldahl analyses, mean of two samples of ca. 50 leaves).

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A METHOD FOR ESTIMATING BARK SURFACE IN FOREST CANOPIES

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ABSTRACT. A method to measure the amount of twig, branch, and trunk surface in forest canopies rapidly is described. The method uses variable-plot sampling with a forester's cruising prism to estimate the relative amount of surface at different canopy heights. These surface estimates can be subdivided into descriptive categories, allowing a quantitative description of surface distribution.

INTRODUCTION

Forest canopies harbor a tremendous variety and number of organisms. How these organisms are distributed in the canopy's light, moisture, and substrate environments reflects their adaptations to canopy habitats and their functioning within epiphytic communities. Measuring light and moisture gradients is relatively straightforward and has yielded useful insights (e.g., Pittendrigh 1948). In contrast, directly measuring twig, branch, and trunk surfaces dispersed in a forest volume is extremely difficult and tedious. Studies of the relationships between epiphytic organisms and their substrates have been hampered by lack of an efficient way to quantify canopy surface independently of the distributions and abundances of canopy organisms.

This paper describes a method to quantify bark surface in forest canopies and subdivide this surface into descriptive categories. Plots do not have to be laid out or measured individually. Instead, bark surface per unit of ground area is inferred from a sample of trunks and branches and certain geometric relationships as explained below. Choosing the sample is done with a cruising prism, which is fast and can be done without being close to each target branch or trunk. The method usually requires unambiguous, yes-or-no decisions making it inherently accurate.

The method is based on a modification of variable-plot sampling, a well-tested technique that has been used by foresters to estimate basal area and volume in timber cruising since it was invented by Walter Bitterlich in the late 1940's. Validation of the original method has been thoroughly documented in a large theoretical and empirical forestry literature (Bell & Dilworth 1989 and references within).

I have used the method successfully in studies of tropical epiphytic plant communities. It could be employed in other canopy studies that need a quantitative description of the relative area and characteristics of bark surfaces. Examples might include studies of bark-gleaning birds, arboreal territories of animals (e.g., ants, lizards), bark beetles, the distributions of other epiphytic plants, studies of forest structure and morphology, the vertical distribution of biomass, and certain studies of tree physiology and morphology. This paper briefly describes variable-plot sampling with a prism, presents a modification that allows prism sampling to be used for estimating surface rather than basal area, and discusses my experience using it in the field.

VARIABLE-PLOT PRISM SAMPLING

Describing a habitat quantitatively usually involves laying out plots of known area within which the presence of a habitat feature is measured. This measure of presence per unit area of plot is assumed to be a random variable with an expected value equal to the feature's presence in the habitat. A count within a unit area of plot is often a sufficient measure of presence if the feature is discrete and individual size is not important (e.g., simple occurrences of plant species, gopher mounds, animal tracks, etc.). Other habitat features, however, may need a measure of size instead of (or in addition to) counts (e.g., vegetation cover, diameter, basal area, etc.). Laying out a number of variously placed plots and then taking counts or counts plus a measure of size, is one way to quantify the presence and environmental distribution of a habitat feature.

In plotless sampling the distances of a sample of objects from a central point can be used to calculate an estimate of object frequency (Greig-Smith 1983). Variable-plot sampling is related to plotless sampling, but the objects included in the sample are determined by both their distances from a central sampling point and by object size. Plot area is adjusted to object size to give each counted object equal weight. A simple tally of such counted objects leads to an estimate of a habitat feature's presence per unit area that incorporates information about object size. Ob-

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