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Insect herbivory in Australian rain forests — is it higher than in the Neotropics?

M. D. LOWMAN

Department of Zoology, University of New England, Armidale, N.S.W., 2351

Abstract

Longterm studies of insect herbivory in Australian rain forest canopies have been conducted from 1979-84, both to determine the levels of grazing within different Australian tree species and also to compare rain forest defoliation with other plant communities, particularly neotropical rain forests. Two methods of measuring herbivory were used in field studies, and one method (longterm observations) measured losses up to five times greater than estimates obtained by the second, more conventional technique of measuring missing leaf area from harvested leaf samples. The longterm measurements were subsequently used to compare herbivory over a range of factors, including light, height, site, species, and individual trees. The patterns of herbivory are discussed in terms of intra- and intercontinental variability. Defoliation studies from the literature are reviewed in terms of their sampling methods employed and in terms of evidence for absolute differences in herbivore abundance.

Introduction

Studies of insect herbivory historically reported fairly moderate, albeit consistent, amounts of defoliation (≈3-10%) in a variety of plant communities, including neotropical rain forests (Odum & Ruiz-Reyes 1970) and northern temperate forests (Bray 1961, 1964). Epidemics of insect pests were exceptional circumstances reported in agricultural or forestry literature, and were usually related to crop situations. More recently, studies of herbivory in plant communities have ranged from negligible amounts (e.g. eucalypt woodlands, Ohmart *et al.* 1983; coral cay vegetation, Lowman 1984a); to moderate levels (e.g. mangroves, Johnstone 1981; neotropical rain forests, Leigh & Smythe 1978); to relatively high levels (e.g. eucalypts, Morrow 1977; neotropical rain forests, Coley 1982); and even epidemic situations (e.g. gypsy moths in northern hardwood forests, Schultz & Baldwin 1982).

To account for this range of variability, there are three possible explanations. First, the apparent differences may be merely artefacts of sampling, since methods vary considerably and have not been critically compared (but see Lowman 1984b). If this is the case, then defoliation levels may be fairly homogeneous among different ecosystems. Second, insect grazing may have such high spatial and temporal variability *within* habitats, that it is impossible to isolate differences *between* habitats with sampling methods that treat defoliation as a discrete event. And thirdly, differences in defoliation levels may be a consequence of absolute differences in the abundance and feeding behaviour of herbivores and/or the palatability of plants. But, only extensive and statistically balanced sampling programmes with accurate sampling methods can reliabily detect differences as per number three.

In this study, the levels of herbivory in Australian rain forests were measured over 5 years, and the results are discussed in terms of the three points mentioned above. Two sampling methods were examined and compared in the field work, and startling differences were obtained between them. The more accurate method was used to conduct an extensive examination of spatial and temporal variation in herbivory among Australian rain forest canopies. In addition, relative abundance of herbivores was measured as a possible explanation of apparent anomolies between Australian rain forests and other continents.

Study areas

Field work was conducted in the canopies of the three major rain forest formations in New South Wales, Australia. Profile diagrams and more extensive site descriptions are listed elsewhere (Lowman 1982a). The three formations, described according to Webb's (1959) classification, included the following sites:

1. Cool temperate rain forest or microphyll fern forest in New England National Park (30°30'S), a montane rain forest situated at 1200 m on the New England Plateau and predominated by one species *(Nothofagus moorei,* Antarctic bech) in the canopy, with 5-10 understorey trees (including *Doryphora sassafras);*
2. Warm temperate rain forest or simple notophyll vine forest located in Royal National Park (34°10'S) with a canopy composed of 10-15 major species (including *D. sassafras, Toona australis* and *Ceratopetalum apetalum);* and
3. Subtropical rain forest or complex notophyll vine forest located in Dorrigo National Park (region 1) (30°20'S) and Mt. Keira Reserve (region 2) (34°30'S), whose canopies have high species diversity (> 30 species including *Dendrocnide excelsa, Doryphora sassafras,* and *T. australis)* and whose structural features were the most complex of the three formations examined. Similar studies in tropical rain forests of Queensland are underway, but the results will not be listed here.

All species that occupied a major portion (> 5%) of the canopy were sampled for herbivory, plus other species where time permitted. In addition, five species that dominated particular rain forest formations were selected for detailed observations over three years: *C. apetalum,* a common canopy species in the warm temperate formation; *D. sassafras,* a canopy dominant in the subtropical and warm temperate formations, and an understorey species in the cool temperate formation; *Dendrocnide excelsa,* a canopy dominant in the subtropical rain forest; *N. moorei,* forming a monospecific canopy in the cool temperate rain forest; and *T. australis,* a canopy species in the subtropical and warm temperate formations. In addition to their importance as canopy species in the rain forests, these species represented a range of leaf morphology and phenology (including soft and hard leaves, glaucous and hairy, evergreen and deciduous, etc.) that may be important in terms of grazing activities.

Sampling methods

Preliminary leaf samples were collected in order to statistically determine the variability of leaves within and among the canopies of the major species. These pilot studies were used to define distinct 'leaf populations' within the canopies, and enabled the establishment of a balanced sampling programme for the measurement of herbivory. This involved the collection of thirty randomly selected mature leaves from different sections of the canopies of all five species. Leaves were picked or shot down with a slingshot from the higher regions of the canopies. Samples were collected with respect to five environmental factors: light (sun versus shade), height, site, aspect, and individuals (trees). Leaf length and leaf area were measured and compared, since these two variables represent morphological features that vary with subtle differences in environmental conditions of a canopy (Raunkier 1934, Larcher 1975, Grubb *et al.* 1963). It is assumed that differences in environment and leaf morphology among regions of the canopy may also affect insect herbivory. The data were subjected to multiple factor analyses of variance, with data transformed to log $(x+1)$ to obtain homogeneity of variance as indicated by Cochran's Test, and significant differences were ranked by Student-Neuman-Keuls tests of mean values (Snedecor & Cochran 1967).

Herbivory was measured using two methods, termed "discrete" and "long-term" sampling. *Discrete sampling* involved the harvesting of at least 200 mature (>1 year old) leaves of each species. For each species, different leaf populations were sampled in multiples of 30 leaves, each leaf population representing a canopy region of a specific light regime, height, individual, or site. All leaf populations together constituted the herbivory for one species. To obtain reasonable standard errors, the numbers of leaves sampled was greater in cases where grazing was highly variable among leaves in one sample. Most samples were collected between January and March 1980 and repeated during 1981 to compare annual variability. The month of collection was not considered a critical factor, however, as long as only mature leaves were sampled. Rain forest leaves are most heavily defoliated during their first three months (Lowman & Box 1983); after maturation, defoliation is not significantly different between months (Lowman 1982a). Senescing leaves were avoided, since decaying leaf tissue can result in formation of leaf holes.

Leaves were harvested, sealed in plastic bags, and refrigerated until measurements of leaf area were made. The actual leaf area (ALA) of 1 surface of each leaf was measured with a Lambda portable area meter (Model 300). The holes in the leaf surface then were covered with heavy tape and the leaf was measured again to determine potential leaf area (PLA), which is the total leaf surface prior to grazing. Then,

$$(1.00 - \frac{\text{ALA}}{\text{PLA}}) \times 100 = \% \text{ leaf area lost to herbivores}$$

This value represents a direct measure of the amount of mature canopy missing, although it may be proportionally larger than the actual increments consumed by the herbivores when the leaves were young (Reichle *et al.* 1973). The use of proportions was considered a more useful expression than actual areas (cm^2) since it was comparable among samples, regardless of leaf size variability; also, proportions of leaf hole remain constant before and after leaf expansion (Lowman 1982a).

Long-term observations involved monitoring permanently marked branches over four years (1979-83) to record leaves completely defoliated. Complete defoliation cannot be accounted for without repeated observations of marked leaves. For each species, at least three branches were marked at different heights and light regimes for three individual trees in at least two sites. Three branches were marked at every 10 m interval (or as near as possible) up canopy trees including both sun and shade canopy regions. Ropes and technical climbing gear were used to gain access to the upper canopy (Perry 1978, Lowman 1982a). Leaves were numbered sequentialy from the base upwards on branches that usually consisted of 8-15 leaves. Numbers were marked on the adaxial leaf surfaces with waterproof Pentel pens. The ink usually lasted at least one year before fading, at which time the numbers were remarked. New leaves were marked as they emerged. Monthly observations were made, and each leaf was measured for changes in leaf area missing, as well as other aspects of mortality and growth.

To measure monthly increments of grazing without harvesting the leaves, a leaf tracing was made and the hole portions were calculated in the laboratory using the area meter (Lambda Model 300). Complete defoliation was distinguished from natural sensecence by observation: older leaves that remained intact for several years and suddenly disappeared were recorded as having senesced; young leaves in which holes increasingly appeared over several months during times of herbivore activity (usually an obvious progression from 0% to 25% to 60-70% to 100%) were considered eaten.

The data on leaf survivorship and monthly herbivory losses were collectively analyzed. Detailed temporal and spatial variation in defoliation is reported elsewhere (Lowman, 1985) and the sampling techniques are also compared extensively in Lowman (1984b). However, average defoliation levels are compared between sampling methods, and on different spatial and temporal scales. These are discussed with respect to the results of other herbivory studies.

The relative abundance of insect herbivores was measured with standardized sampling techniques on a repeated basis in a number of sites. The methods are described elsewhere (Lowman 1982, 1984b), and the results are referred to in comparisons of Australian herbivores with other rain forests.

Results

1. *Pilot Samples to Determine Sampling Regimes*

The results of the pilot samples to determine leaf 'populations' within the canopies of the five species are summarized in Table 1. There was a wide range of variability in leaves among different regions of the canopy, as affected by light, height, site, individuals, or aspect. *T. australis* and *D. excelsa* have fairly homogeneous canopies, with no significant differences in leaf length or area with respect to any of the five environmental factors. The sampling design for measuring leaf survival and herbivory in their canopies, therefore, required no extensive subsmpling within different sections; rather, all leaves in 1 tree were lumped as one sample. Conversely, *N. moorei* exhibited variability with respect to height and light, necessitating a sampling regime that included branches along vertical transects through the canopy in both sun and shade regions. The canopies of *C. apetalum* and *Doryphora sassafras* exhibited the greatest variability of leaves within their canopies, and thus required the most extensive sampling to measure herbivory within each different portion of canopy.

TABLE 1. Results of analyses of variance of leaf length and leaf area — determination of leaf "subpopulations" within and among rain forest canopies (n = 30).

Species	*light*	*height*	*aspect*	*among individuals*	*among sites*
N. moorei	** sun < shade	** 10 = 5 < 1 m	N.S.	N.S.	N.S.
Doryphora sassafras	*** sun < shade	*** 20 < 10 = 1 m	N.S.	N.S. (RNP: *)	* NEP < DNP = Mt. K. < RNP
C. apetalum	*** sun < shade	** 20 < 10 < 1 m	N.S.	N.S.	* DNP = Mt. K. < RNP
Dendrocnide excelsa		N.S.	N.S.	N.S.	N.S.
T. australis	N.S.	N.S.	N.S.	N.S.	N.S.

RNP = Royal National Park
DNP = Dorrigo National Park
NEP = New England National Park
MT. K = Mt. Keira Boy Scout Preserve

* indicates $P < 0.05$
** indicates $P < 0.01$
*** indicates $P < 0.001$

2. *Difference between Sampling Methods*

A comparison of the two sampling methods — discrete and long-term — showed that discrete samples give a more conservative estimate of herbivory than the long-term observations (Table 2). This indicates that insects consume some leaves entirely rather than only partially grazing each leaf. The discrepancy between methods ranged from negligible differences *(T. australis,* where the longterm/discrete ratio was 1.1) to a highly significant ratio of 5.0 for sun leaves of *C. apetalum,* where many leaves were entirely eaten. Overall, the longterm observations revealed a discrepancy approximately 2.5 times greater than the discrete sampling. All further sampling of herbivory both within and among different Australian rain forests utilized the longterm method.

3. *Temporal and Spatial Variability in Grazing*

Within the canopies of individual species, herbivory varied spatially with respect to light, height, and site; and temporarily with respect to months, years, and age of leaves. These results are reported in detail elsewhere (Lowman 1982a), but are summarized here. In general; shade leaves ere grazed more heavily than sun leaves (e.g. *Doryphora sassafras:* $F_{1,58} = 5.89$, $0.05 > P > 0.01$; Fig. 1 and Table 3); leaves near the ground were defoliated more extensively than in the upper canopy, (e.g. *C. apetalum.* $F_{2,72} = 4.13$, $0.05 > P > 0.01$); and site differences existed on both a small scale (e.g. *N. moorei* among three subsites: $F_{2,11} = 3.03$, $0.01 > P > 0.001$), although not significantly over a larger geographic scale (e.g. *D. sassafras* among three rain forest formations: $F_{2,117} = 0.55$, n.s., but see Table 3). In addition, all species showed

TABLE 2. Differences between two sampling methods for measuring herbivory in Australian rain forest canopies

leaf sample	*longterm*	*discrete*	*discrepancy*	
			L/D	*Significance*
Toona australis — Dorrigo	6.3	5.7	1.1	N.S.
— Mt. Keira	3.3	2.9	1.1	N.S.
Dendrocnide excelsa — Dorrigo	32.5	16.5	2.0	**
Ceratopetalum apetalum — Royal, sun leaves	16.9	3.4	5.0	**
— Royal, shade leaves	35.3	9.4	3.8	**
Nothofagus moorei, New England — subsite 1	22.5	11.7	1.9	*
— subsite 2	40.5	15.0	2.7	**
— subsite 3	30.3	13.6	2.2	**

*$0.05 > P > 0.01$
**$0.01 > P > 0.001$

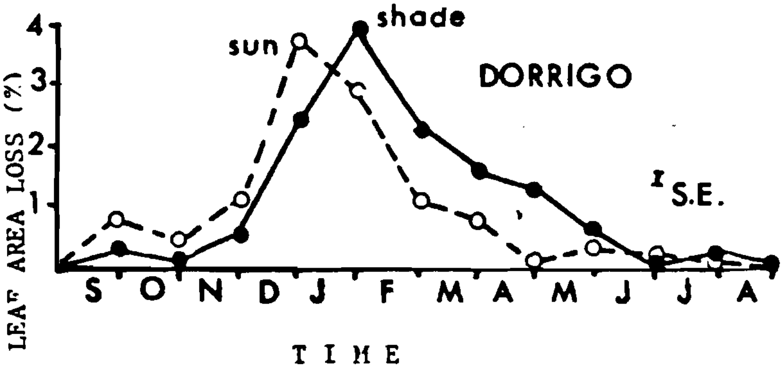

Fig. 1. Monthly herbivory losses for leaves of *Doryphora sassafras* in Dorrigo National Park, N.S.W., showing the differences between sun and shade regions of canopy (expressed as mean proportion grazed per leaf each month). Average annual leaf area losses are 13.4% (sun) and 16.3% (shade), and differ significantly ($F_{1,58}=5.89$, $0.05>p>0.01$).

variability in proportions grazed from month to month (Fig. 1), with most defoliation during the summer months when herbivores were most abundant (Lowman 1982b). Young leaves were preferred over old leaves, due probably to their softer, more palatable tissue (Lowman & Box 1983). For example, approximately 54% leaf area was grazed from young beech leaves, as compared to less than 1% from old leaves (Selman & Lowman 1983).

4. *Variation in herbivory between Australian rain forest formations*

To estimate herbivory for an entire rain forest community (Table 4), the grazing losses of many species and canopy regions were averaged, on a proportional basis according to a species' commonness within a site (Lowman 1982a). The cool temperate rain forest, with its monospecific canopy of *N. moorei,* had the highest levels of grazing, approximately 26% annual leaf area loss. The subtropical forests had the lowest defoliation levels (~ 14.6%), and also required the greatest number of samples due to its high species diversity and range of canopy regions (Fig. 2). The warm temperate was intermediate both in species diversity of its canopy and in grazing (22%).

Discussion

The removal of leaf material by primary consumers at proportions of up to 40 per cent for some Australian rain forest trees is surprisingly high as compared to past results in the literature (Table 5). Most studies in other forest types report primary consumption at 3-10% (Bray 1964, Bray & Gorham 1964, Wiegart 1970, Jordon 1971) and rain forests

TABLE 3. Variation in grazing on sassafras leaves with site, light, and sampling

site	*light*	*longterm*	*discrete*	*sign.*
		sampling		
Cool temperate		13.6	12.0	N.S.
Subtropical	— sun	13.4	4.4	**
	— shade	16.3	6.4	**
Warm temperate	— sun	17.6	4.5	**
	— shade	27.8	7.6	**

*0.05>P>0.01
**0.01> P>0.001

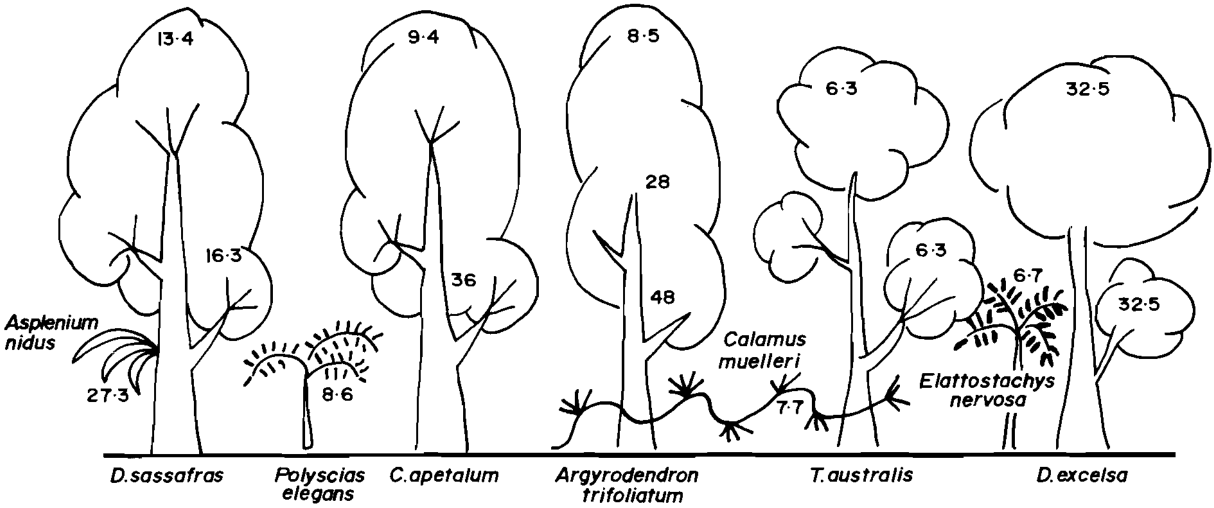

Fig. 2. Herbivory in a subtropical rain forest canopy, NSW Australia, illustrating the changes with height and among species. Herbivory throughout the canopy is approximately 14.6% annual leaf area loss.

are no exception (Odum & Ruiz-Reyes 1970; Leigh & Smythe 1978). In these instances, decay is usually regarded as a larger, more important pathway of leaf turnover, with grazing relatively insignificant in terms of overall community biomass (Hairston *et al.* 1960). However, in an evergreen canopy (where most leaves live more than one year), insect damage to young leaves remains incorporated into the canopy for twice the duration of annually deciduous leaves. An accurate calculation of herbivory requires more than simply measuring discrete amounts of holes in leaves: it requires information on the longevity of leaves, the amounts of damage to different ages of leaves, and the proportions of different leaf cohorts that comprise the canopy. And, if young leaves are sometimes grazed *entirely*, these 100% leaf area losses must also be accounted for.

In this study, three major points arise that ultimately affect any comparisons made between Australia and other continents. These include sampling techniques and the possible underestimates that may result with discrete samples; intrinsic variability within different portions of rain forest canopies (particularly where studies have not adequately sampled a range of species and canopy regions); and thirdly, the factors that may lead to underlying differences in defoliation (e.g. herbivore abundance or leaf palatability). Unless we have explored all three

TABLE 4. Differences in herbivory among three Australian rain forests

Rain forest	*Longterm Sampling* (*% leaf area grazed/year*)	*Discrete Sampling*	*Discrepancy* *L/D*	*sign.*
Cool Temperate	26.0	12.7	2.0	**
Warm Temperate	22.0	6.2	3.5	**
Subtropical	14.6	8.3	1.8	*
$\bar{X}$	20.9	9.1	2.3	

*0.05> p>0.01
**0.01> p> 0.001

TABLE 5. Studies of rain forest herbivory and other tropical forests

Site	*Study*	*Method*	*Leaves Sampled*	*Measuring Technique*	*% Grazed Annually*
AUSTRALIA					
— Cool temperate	Lowman 1984	Longterm, 5 yr; Discrete for 100+ species	Low/High, sun/shade, young/old, 5 species, 4 sites.	Area meter	26
— subtropical	Lowman 1984				22
— Warm temperate	Lowman 1984				14.6
NEW GUINEA	Wint 1982	Discrete	100 sun leaves at 20-30 m	Visual ranking: 5 classes	9-12
AMERICAS					
— Costa Rica, ferns	Hendrix & Marquis 1983	Discrete	Fronds	Xerox, cut & weigh	5.5-9.9
trees	Stanton 1975	Discrete	100 leaves, 24 plants of 2 forests, young/old	Visual ranking: 4 classes.	7.5 (new) 30 (old)
— Panama	Wint 1982	Discrete	100 leaves at 20-30 m	Visual ranking: 5 classes.	13
— Barro Colorado	Leigh & Smythe 1978	Neither	Littertrap weights & data from other studies	Calculations	8 (6 insect; 1-2 vertebrates)
	Odum & Ruiz-Reyes 1970	Discrete	Littertrap leaves	Photo-technique	7.8
	Coley 1982	"Longterm": 2-3 month monitoring at intervals	Saplings: 21 pioneer & 21 persistent species, 1700 leaves.	Counted squares on grid	21 (up to 190)
	Leigh & Windsor 1982	Neither	Littertrap weights	Calculations	15
— Puerto Rico	Benedict 1976	"Longterm": collected leaves after 2-3 months	50 tagged leaves of major species, 3 sites	Area meter	5.5-16.1
MANGROVES					
— Australia,					
open canopy	Saenger, pers. comm.	Observations	—	—	5%
closed canopy	Saenger, pers. comm.	Observations	—	—	25%
— New Guinea	Johnstone 1981	Discrete	Random branches of 28 species	Area meter	$\bar{x}$ 6.8%
— South Florida,					
high nutrient	Onuf *et al.* 1977	"Longterm": fortnightly for 1 year	Leaves observed during fieldwork	Visual estimates	21
low nutrient					8

TABLE 6. Abundance of herbivores in rain forests of the world

Site	*Study*	*Methods*	*Abundance of herbivores (% of total insects)*
AUSTRALIA — NSW, Qld	Lowman 1984	Sweeps (spring, summer)	15.4%
		Sweeps, light, trays (year)	34.1
— NSW	Lowman 1982	Sweeps (year)	9
		Sweeps & light (year)	23
PAPUA NEW GUINEA	Wint 1982	Casual observation	—
AFRICA — Zaire	Sutton & Hudson 1980	Light traps	≈ 48
— Nairobi	Denlinger 1980	Malaise trap	—
— S. Africa	Southwood *et al.* 1982	Knockdown insecticide (6 exotic plant species)	26
AMERICAS — Hawii	Gagne 1979	Knockdown insecticide	11 (of species)
— Costa Rica	Janzen & Schoener 1968	Sweep nets	≈ 56 (Coleoptera≈ 42)
— Barro Colorado	Smythe 1982	Light: 2hr/4 nt/wk	—
	Wolda 1978	Light: every nt 1974-77	—
	Leigh & Smythe 1978	Calculations & Litter traps	Herbivores: 85% insect 15% verteb
	Elton 1973	Trays, nets, sucking	≈ 30
— Mocambo	Elton 1973	Trays, nets, sucking	≈ 31
NORTHERN HARDWOODS			
USA — (Tennessee)	Whittaker 1952	Sweep nets, summer	≈ 26
ENGLAND	Southwood 1982	Knockdown insecticide	≈ 56

explanations of observed differences, we can not be sure that Australian rain forest herbivory is indeed different from other continents.

The discrepancies of discrete sampling have been illustrated. For species where entire leaf consumption by herbivores is a rare event (e.g. *T. australis),* then discrete sampling is an efficient and accurate method of measurement. But, for species whose leaves are often eaten entirely by grazers (e.g. *Doryphora sassafras),* discrete samples underestimate primary consumption by as much as two- or threefold. The herbivory levels of Australian rain forests, as measured by longterm sampling, are higher than most studies in other rain forests (Table 5). Unfortunately, however, it is difficult to make direct comparisons among studies in the literature due to the variety of sampling methods in evergreen complex canopies, with different canopy regions making it difficult to assume that samples are representative of the entire canopy. Also, some studies used longterm observations but sampled only in the understorey or in saplings, whose leaves may be quite different from upper canopy trees. It is interesting to note, however, that the only quantitative estimates which were relatively high (i.e.> 15%) and similar to Australian results utilized longterm sampling (Benedict 1976; Coley 1982).

In addition to the problems of sampling artefacts, one cannot ignore the additional difficulties that relate to measuring variables in such a complex habitat. No other forest type has such a wide range of canopy regions, changing with light, height, altitude, species, and even individuals. In Australia, significant differences in grazing intensities occurred with 5 major factors: age of leaves, species, light, height, and site. In the neotropics, Coley (1982) illustrated huge differences between the grazing incurred by persistent versus pioneer species. And, Hendrix & Marquis (1983) showed up to twofold differences in herbivory of three fern species which all presumably grow within homogeneous climates at ground level. Studies of herbivory in rain forests require a wide range of species and canopy regions in the sampling, in order to account for the wide range of spatial variability.

And thirdly, if all constraints of samples and variability are satisfied, the apparent higher herbivory levels in Australian rain forests should be further supported by trophic and physiological differences between Australia and the Neotropics. It has been suggested that the proportions of herbivores, particularly Coleoptera, may be higher in Australia as compared to the rest of the world

(Morrow, 1977; Lowman 1982b; Heatwole, pers. comm.). Table 6 is a summary of some insect surveys in rain forests, with comparative data on the relative abundance of herbivores. As with the methods of measuring defoliation, the field methods of insect sampling have also been extremely variable.

It is difficult to extract data on the relative abundance of trophic levels of insects (e.g. herbivores) when studies have often been aimed at one major taxon (e.g. Psocids, Broadhead 1983; and Hemiptera, Rees 1983); and general insect surveys in the tropics have usually encompassed small temporal and spatial scales (reviewed in Wolda 1983). Despite these drawbacks, some studies are extremely comprehensive, such as Erwin's (1983) fogging studies where he collected 24,108 insects from 4 types of forest in Brazil, with 36% herbivorous orders (but 79% if ants are included, some of which are leaf-eating in the neotropics). It still remains difficult, however, to make comparisons between studies, unless field methods are both standardized and easy to repeat elsewhere. Some longterm data are becoming available (e.g. Wolda 1983 on Homoptera at Barro Colorado Island); and some studies have used one standard sampling technique (e.g. light traps: Sutton & Hundson 1980 in Zaire; Sutton, Ash & Grundy 1983 in Brunei; and Sutton 1983 in Sulawesi). These studies provide important information on temporal and spatial variability of insect groups in the tropics.

For general trophic comparisons, however, insect surveys repeated over many seasons collected by standard techniques are lacking in the existing literature (Table 6). It is difficult to estimate the abundance of herbivores, since species are not always listed by their trophic level. When not listed specifically in the literature, I totalled Hemiptera, Coleoptera, Phasmatodea, and Orthoptera, which may overestimate herbivores in some cases (e.g. frugivorous beetles), and underestimate them in others (e.g. leaf-cutting ants (Hymenoptera) in the neotropics).

Due to the uncertainties of comparing studies that utilize a range of methods, it is impossible to conclude whether Australian rain forests are different from other forests. According to the majority of reported results (e.g. northern temperate forests, mangroves, most neotropical rain forests), defoliation in Australian rain forests is higher by two- or threefold. But, when compared to the few studies where longterm observations were conducted (e.g. Coley 1982, 1983), the apparent differences are negligible. The variability in insect grazing patterns throughout a rain forest canopy is enormous, and the time periods required to properly monitor these plant-insect relationships are extensive. I suggest that we concentrate upon conducting standardized, comparative studies: comprehensive insect sweeping and light-trapping between rain forests; leaf chemical analyses of the common and persistent species; and meanwhile, begin the longterm observations that are required to accurately measure primary consumption.

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