Herbivory in Australian Forests — A Comparison of Dry Sclerophyll and Rain Forest Canopies

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Long-term measurements of insect grazing in the canopies of different Australian forest types were compared over 10 years. Forest types included rain forests (cool temperate, warm temperate, and subtropical) and dry sclerophyll, all situated within a 50 km radius of Armidale, New South Wales. Similar methods of marking and measuring leaves in tree canopies were employed, and similar modes of analyses were executed after the leaf lifespan was completed. Grazing levels for a forest stand ranged from as low as 5 – 8% annual foliage consumption to 300% (when three successive flushes were grazed). Contrary to earlier literature, this long term, community level study shows that herbivory in forest canopies is extremely variable both at intra- and inter-site spatial scales.

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There awaits a rich harvest for the naturalist who overcomes the obstacles — gravitation, ants, thorns, rotten trunks — and mounts to the summits of jungle trees.

William Beebe, 1917, Tropical Wild Life

When I first came to Sydney University as a post-graduate student, I was very keen to study the rain forest canopy. In fact, I hoped to construct a swing and dangle precariously up in the foliage to survey butterfly populations. Having a much better understanding of the statistical requirements for ecology and the necessity of replication in sampling design, Peter Myerscough kindly talked me out of waiting for elusive pollinators in the upper canopy. I decided to study leaves instead, and they presented themselves as much better replicated units for sampling, so important for my first research endeavor.

I then had to work out some protocols for working in that ecological frontier: the forest canopy. I contemplated hiring monkeys to fetch my leaves from the upper crowns (or any other mode other than dangling precariously from a limb by myself), but Peter kindly informed me that learning to climb was my best option. Frightened though I was, that advice has carried me through over fifteen years of intensive research (subsequently using many other methods of access) on many aspects of leaves in forest canopies. I am grateful to Peter for his friendship, advice and collegiate interactions over those many years, and I hope — as his student — to continue his legacy of excellence in ecology.

INTRODUCTION

The consumption of plant material by herbivores is a subject of great economic as well as ecological importance (reviewed in Barbosa and Schultz, 1988; Price *et al.*, 1991). The most abundant herbivores in forests are insects, and Australia is no exception (see Morrow, 1977; Lowman, 1985). The impact of herbivory on a plant ranges from stimulation of new growth (reviewed in Mattson and Addy, 1973; Lowman, 1982) to negligible impacts (Lowman, 1984a) to entire stand dieback (Lowman and Heatwole, 1992).

Insect herbivores in forests are difficult to study, due both to their relatively small size as well as to their cryptic qualities in a large three-dimensional space (reviewed in

Lowman and Moffett, 1993). When walking through a forest, we usually focus our observations on a narrow band of green foliage, from about 0 – 2 m in height. This represents at most 10% of the foliage in mature forests, with the rest often high above our heads and consequently beyond our observations. Since the majority of plant-herbivore relationships occur where the foliage is located, it is obvious that herbivory as a forest process remains literally out of reach. Only recently have techniques of access been developed to facilitate research in forest canopies.

It has been previously reported that forests represented vast expanses of homogeneous green tissue (e.g. Hairston, Smith and Slobodkin, 1960), but this assumption is over-simplified. The life of a leaf, which comprises the building block of the forest canopy, undergoes many complex and critical phases of growth dynamics, including leaf emergence, longevity, and physical qualities that affect its susceptibility to herbivory, decomposition, and senescence. In a leaf's life span, it is critical to survive the vulnerable weeks of foliar expansion without being eaten (Coley, 1983; Lowman, 1985). From a plant's perspective, there exists an evolutionary roulette of rendering one's green foliage less susceptible to successive generations of defoliators. Viewed from the point of view of a herbivore, a complex world of different bites must be recognized: soft versus tough, nutritious versus non-nutritious, old versus young, apparent versus non-apparent, rare versus common, and probably other choices that have not yet been detected by biologists (reviewed in Lowman, 1994).

Recently, the importance of understanding insect pests in forests has led to increased research on canopy defoliation (e.g., Barbosa and Schultz, 1987, Wong *et al.*, 1991; Lowman and Heatwole, 1992). In Australia, the topic of forest herbivory has fostered lively debates, particularly concerning whether or not higher levels of herbivory exist as compared to other systems (see Lowman, 1987; Fox and Morrow, 1983; Landsburg and Ohmart, 1989). Because of the variability of methods employed to measure herbivory (*sensu* Lowman, 1984), the question still remains: does Australia indeed sustain higher levels of herbivory in its forests as some data indicate, or have studies in these systems simply been conducted during phases of outbreak, or are some methods employed less accurate than others?

Historically, most herbivory studies have involved the measurement of levels of defoliation in forests at one point in time. Foliage was typically sampled near ground level in temperate deciduous forests, where annual losses of 3 – 10% leaf surface area were reported (reviews in Bray and Gorham, 1964; Landsberg and Ohmart, 1989). Most studies, however, could not be extrapolated to evergreen rain forests for three reasons: 1.) temperate deciduous forests have a comparatively simple phenology with an annual turnover of leaves (e.g. Bray, 1961); 2.) measurements were sometimes made from senescent leaves retrieved from the forest floor (Odum and Ruiz-Reyes, 1970); and 3.) only destructive discrete sampling was attempted (e.g. Leigh and Smythe, 1978). In short, defoliation was treated as a discrete, snapshot event (Diamond, 1986), accounting for neither temporal nor spatial variability.

In recent years, the complex temporal and spatial patterns of leaf growth dynamics in forest canopies have caused ecologists to expand their sampling designs. For example, the traditional methods of measuring herbivory by destructive sampling of small quantities of leaves have been expanded (reviewed in Lowman, 1984b; Landsburg and Ohmart, 1989). Whereas earlier measurements of forest herbivory were conducted over short time spans, were restricted to understory foliage, and involved very little replication within and between crowns, more recent studies have incorporated larger sampling regimes. And, when herbivory was monitored over longer periods (> 1 yr) and included wider ranges of leaf cohorts (including different age classes, species, and heights), higher levels of grazing were reported (Coley, 1983; Lowman, 1985; Lowman and Heatwole, 1992). Long-term measurements have also illustrated the high variability of herbivory, both temporally and spatially, within a stand (e.g. Coley, 1983; Lowman, 1985; Brown and Ewel, 1987; 1988).

In this study, I compare aspects of the spatial and temporal heterogeneity of herbivory between adjacent rain forest and dry schlerophyll tree crowns within New South Wales, Australia, (but the comparisons between Australia and other continents are still open to debate). I also emphasize the methodological challenges associated with studies of herbivory as a canopy process (because obviously the reliability of methods has an enormous impact on the accuracy of the results). Whereas biologists have successfully counted and measured the abundance of herbivorous molluscs on a two-dimensional system such as intertidal rocky shores (e.g., Underwood and Denley, 1984) the height and structural complexity of forest canopies make it more difficult to count and measure grazing impacts there.

METHODS

At least two representative stands of each of six different types of Australian forest were selected for field work. These were classified as wet forest: cool temperate, warm temperate, and subtropical rain forests; and dry forest: healthy sclerophyll forest, rural stands of eucalypts that typify the outback environment, and dieback stands of eucalypts that have recently come to dominate the agricultural landscapes throughout Australia (see Lowman, 1982; and Lowman and Heatwole, 1992 for further site descriptions). All of the forests were situated within 50 km of Armidale, New South Wales, at approximately 30° 20' S.

At least five tree species from wet and from dry forests were selected for field measurements. Both common and rare species were selected in each forest type, since the overall aim was to examine herbivory at the community level. For obvious logistic reasons, it was not possible to measure the canopies of all tree species; but in some cases, adjacent trees to the study samples were also measured. Trees that were studied in greatest detail included:

rain forests — *Ceratopetalum apetalum* D. Don (Cunoniaceae), *Doryphora sassafras* Endl. (Monimiaceae), *Dendrocnide excelsa* (Wedd.) Chew (Urticaceae), *Nothofagus moorei* F. Muell. (Fagaceae), and *Toona ciliata* (F. Muell) Harms (Meliaceae);

and dry forests — *Eucalyptus blakelyi* Maiden, *E. viminalis* Labill, *E. melliodora* A. Cunn. ex Schauer, *E. caliginosa* Blakely and McKie, and *E. nova-anglica* Deane and Maiden.

Leaf growth and herbivory was measured monthly for 5 years in wet forests (1979-1984) and dry forests (1983-1988). Because of the longevity of the evergreen leaves of some species (e.g. *D. sassafras* leaves lived between 2 – 12+ yrs, Lowman 1992), more than five years of field measurements were made on some of the rain forest trees. Leaf cohorts were marked in the canopy representing different light regimes, heights, species, individual crowns, and sites. In total, over 10,000 leaves were monitored over the duration of their lifespans. Isolated events in the life of a leaf were quantified, including date of emergence, length of survival, proportion of leaf-area losses to herbivores, date of senescence, and rate of decay. Only herbivory is reported here, although other information was necessary to calculate annual levels of grazing.

The extent of replication of leaves within a crown was determined by pilot studies using leaf size to indicate environmentally different regions in the canopy (Lowman, 1985). For example, because *C. apetalum* leaves varied significantly in size with respect to light levels, canopy heights, individual trees and sites, leaves within each of these categories were monitored. In contrast, *D. excelsa* had a homogeneous canopy, so all leaves within each tree were pooled as one population. In general, between 200-1000 leaves were measured to calculate herbivory for a species. Further information on the numbers of replicates and regions of crown sampled for both wet and dry forest are reported elsewhere (Lowman, 1992; Lowman and Heatwole, 1992, respectively).
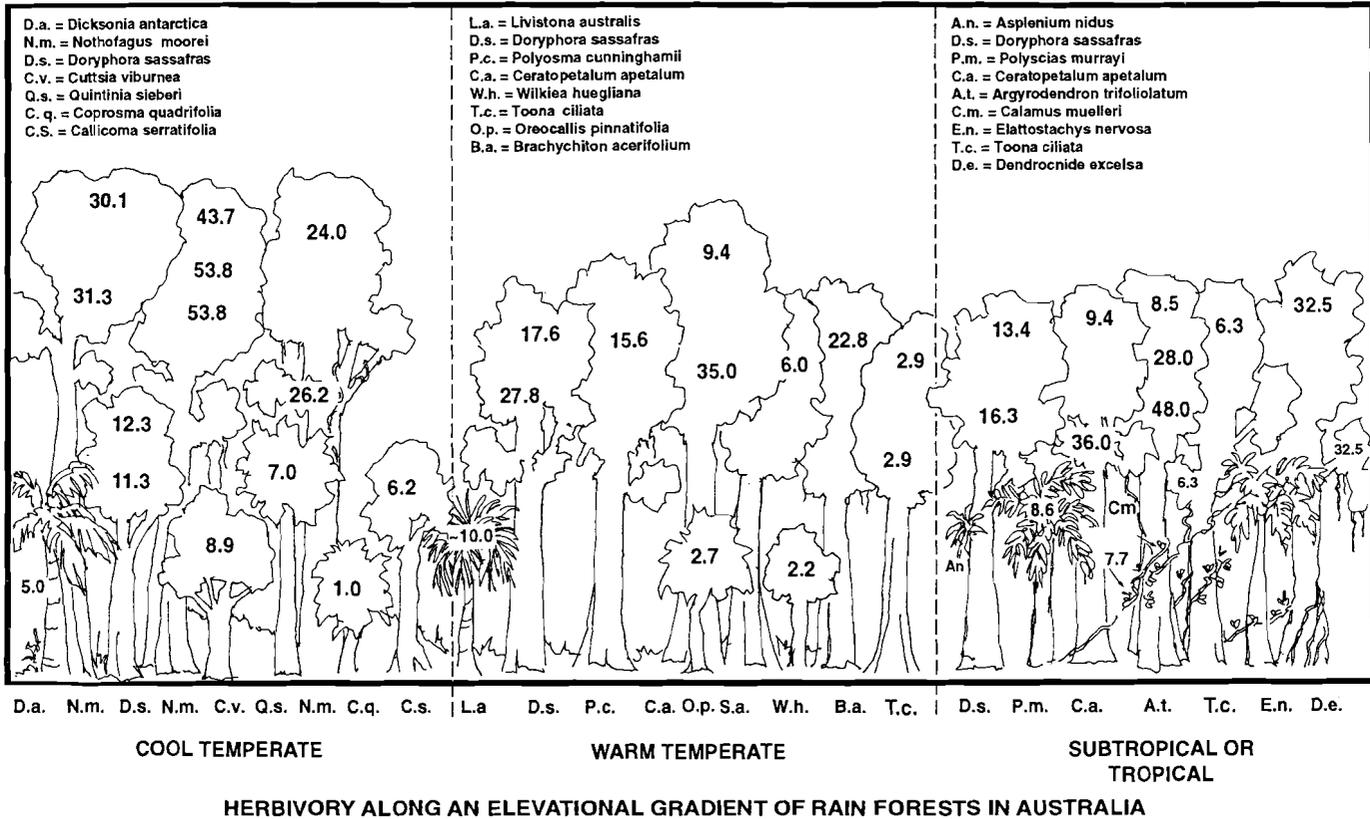
D.a. = Dicksonia antarctica
N.m. = Nothofagus moorei
D.s. = Doryphora sassafras
C.v. = Cuttsia viburnea
Q.s. = Quintinia sieberi
C.q. = Coprosma quadrifolia
C.S. = Callicoma serratifolia

L.a. = Livistona australis
D.s. = Doryphora sassafras
P.c. = Polyosma cunninghamii
C.a. = Ceratopetalum apetalum
W.h. = Wilkiea huegliana
T.c. = Toona ciliata
O.p. = Oreocallis pinnatifolia
B.a. = Brachychiton acerifolium

A.n. = Asplenium nidus
D.s. = Doryphora sassafras
P.m. = Polyscias murrayi
C.a. = Ceratopetalum apetalum
A.t. = Argyrodendron trifoliolatum
C.m. = Calamus muelleri
E.n. = Elattostachys nervosa
T.c. = Toona ciliata
D.e. = Dendrocnide excelsa

D.a. N.m. D.s. N.m. C.v. Q.s. N.m. C.q. C.s. | L.a D.s. P.c. C.a. O.p. S.a. W.h. B.a. T.c. | D.s. P.m. C.a. A.t. T.c. E.n. D.e.

COOL TEMPERATE   WARM TEMPERATE   SUBTROPICAL OR TROPICAL

HERBIVORY ALONG AN ELEVATIONAL GRADIENT OF RAIN FORESTS IN AUSTRALIA

Fig. 1. Herbivory (expressed as a proportion of annual leaf area losses) throughout different rain forest communities in New South Wales, Australia.
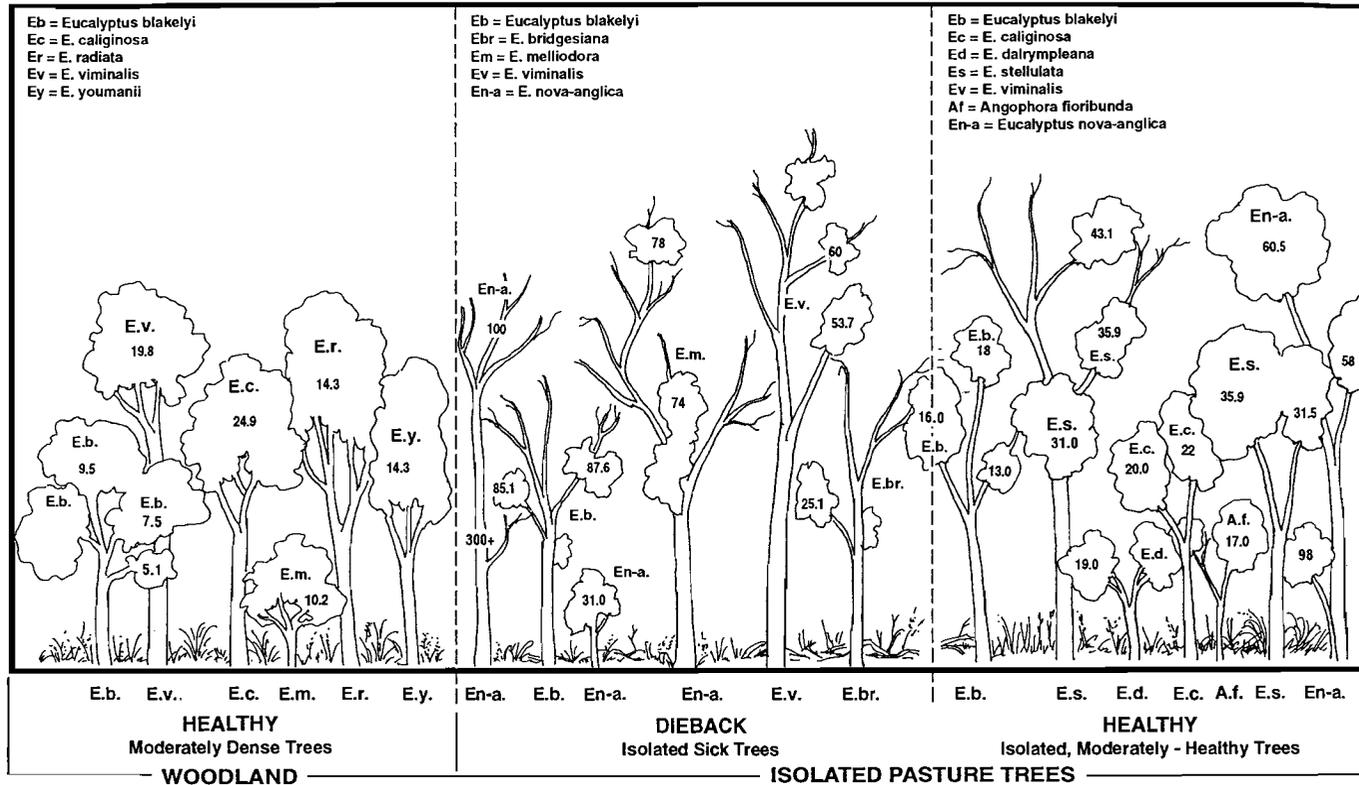
Eb = Eucalyptus blakelyi
Ec = E. caliginosa
Er = E. radiata
Ev = E. viminalis
Ey = E. youmanii

Eb = Eucalyptus blakelyi
Ebr = E. bridgesiana
Em = E. melliodora
Ev = E. viminalis
En-a = E. nova-anglica

Eb = Eucalyptus blakelyi
Ec = E. caliginosa
Ed = E. dalrympleana
Es = E. stellulata
Ev = E. viminalis
Af = Angophora floribunda
En-a = Eucalyptus nova-anglica

E.v. 19.8
E.r. 14.3
E.c. 24.9
E.y. 14.3
E.b. 9.5
E.b. 7.5
E.b. 5.1
E.m. 10.2

En-a. 100
78
E.v. 53.7
E.m. 74
87.6
85.1
E.b.
300+
60
16.0
E.b. 13.0
E.b.
25.1
E.br.
En-a. 31.0

En-a. 60.5
43.1
35.9
E.s.
E.b. 18
E.s. 35.9
E.s. 31.0
E.c. 22
E.c. 20.0
58
31.5
19.0
E.d.
A.f. 17.0
98

E.b. E.v. E.c. E.m. E.r. E.y. | En-a. E.b. En-a. En-a. E.v. E.br. | E.b. E.s. E.d. E.c. A.f. E.s. En-a.

HEALTHY
Moderately Dense Trees

DIEBACK
Isolated Sick Trees

HEALTHY
Isolated, Moderately - Healthy Trees

WOODLAND ————————————————— ISOLATED PASTURE TREES

Fig. 2. Herbivory (expressed as a proportion of annual leaf area losses) throughout different dry sclerophyll forest communities in New South Wales, Australia.

Profile diagrams were constructed throughout several forest sites for each forest type, using a hypsometer and standard forestry techniques (see Lowman, 1982). Idealized forest diagrams were constructed from these measurements, and used here to map the herbivory within each forest community.

RESULTS

Averages of leaf surface area loss of all the leaves were calculated and mapped to illustrate the herbivory for each forest community (Figs. 1, 2). Herbivory in individual canopies ranges from negligible (e.g. < 3% for *Toona ciliata*) to over 300% of annual foliage production in dry sclerophyll trees where some eucalypts re-foliated three successive times after defoliation (see also Lowman and Heatwole, 1992). Herbivory levels varied significantly both between species and between forest types, with the dieback stands exhibiting the highest grazing levels, some to such extremes that crown mortality was also observed.

Herbivory in rain forests was quite different from neighbouring dry sclerophyll canopies. In rain forests, there were greater differences with vertical stratification from top to bottom of the canopy. For example, *Ceratopetalum apetalum* had 9.4% leaf area grazed in the upper canopy, as compared to 35% in the understory of the warm temperate rain forest, almost a 4-fold difference. In contrast, eucalypt trees had more homogeneous herbivory throughout the crown of each individual; but more wide-ranging levels of grazing between species and sites. Some trees in dry sclerophyll woodlands lost as little as 8% leaf area per year (e.g. *Eucalyptus blakelyi*), whereas *E. nova-anglica* in rural pastures lost as much as 300% in a given year (i.e. scarab beetles ate the entire crown three times successively, followed by re-leafing). Although the dietary qualities of eucalypt foliage have been studied elsewhere (see Landsburg, 1990; Fox and Morrow, 1983), it is nonetheless phenomenal that levels of grazing vary so enormously among neighbouring trees.

In order of increasing levels of annual grazing, Australian temperate forests were ranked as follows: healthy dry sclerophyll woodlands (13%), subtropical rain forests (14%), warm temperate rain forests (22%), cool temperate rain forests (27%), healthy stands of sclerophyll trees in rural pastures (35%), and dieback sclerophyll trees in rural pastures (89%).

DISCUSSION

The measurement of herbivory in evergreen forest canopies may be more complicated than predicted before canopy access was a reality, because the cycles of leaf turnover are not always seasonally distinct (e.g., Lowman, 1992). The existence of many cohorts or leaf populations within one crown, requires a more complex sampling design to ascertain both annual defoliation and cumulative herbivory over a leaf's life span. In Australian evergreen forests where leaf longevity was also extremely variable, the canopy was composed of a complex mosaic of different aged leaves, with different susceptibilities to herbivores. Leaf life spans ranged from as short as 4-6 months (e.g., *Dendrocnide excelsa*, Urticaceae) (Lowman, 1992) up to 25 years (e.g. *Araucaria* sp., Aracaceae) (Molisch, 1928). The average age of an Australian subtropical rain forest canopy leaf ranged from 2 – 4 years (sun) to 4 – 12 years (shade) (Lowman, 1992).

Over this ten year period, herbivory was measured using long-term monitoring techniques and repeated visits to measure leaves and their associated phenological changes (see Lowman, 1984b). This long-term sampling yielded grazing levels that were 2 – 3 times higher than those reported in short term studies of other evergreen forests (*cf.* Leigh and Smythe, 1978). It also revealed an enormous difference in grazing sus-

ceptibility between different species and within different leaf cohorts on one tree crown.

So what do these relatively high levels of insect grazing mean in terms of the dynamics of the forest canopy community? First, the variability in levels of grazing are higher than previously assumed, even in adjacent forests. And second, the tolerance of trees to levels of grazing appears much higher than previously thought, and exhibits a plasticity in susceptibility to defoliation that may be very important to subsequent management and regeneration of forest stands.

The tolerance of the dry sclerophyll forest canopies to outbreaks is illustrative of their strong response to stress, probably a consequence of many thousands of years of adaptation to physical (as well as biological) limitations. Conversely, in the rain forest, the environmental 'stresses' may be more subtle within one crown, such as the changes in microclimate as one progresses from ground to upper canopy through the complex layers of foliage. Comparative studies of insects in these two habitats will provide further information on their trophic structures, especially relative proportions of herbivores (Kitching *et al.*, 1993 and unpublished data).

The heterogeneity of defoliation is a consequence of a leaf's environment and phenology, with different leaf cohorts exhibiting different susceptibilities to grazing (*sensu* Whittam, 1981). From these long-term studies of herbivory in forest canopies, I am now able to isolate "hotspots" in the canopy, where grazing will be predictably higher (Fig. 3). These 'hotspots' represent foliage with greatest susceptibility to herbivores, such as new leaf flushes, colonizing species that are characterized by soft tissue, lower shade regions of the canopy where insects aggregate to feed in the absence of predators, and canopy regions that attract more insects due to the presence of flowers, epiphytes or vines (e.g., Lowman, 1992; Lowman, Moffett and Rinker, 1993; Lowman, unpublished). These regions are different between rain forest and dry sclerophyll canopies. In the dry forests, where the physical environment throughout the canopy is less stratified, grazing was more homogeneous throughout the canopy of an individual tree, but entire crowns of some species were grazing hotspots (e.g. *E. nova-anglica*). In contrast, the rain forest canopies exhibit less magnitude of inter-species variation, but obvious grazing preferences within individual crowns (e.g. young leaves in the mid-canopy).

For example, *Nothofagus moorei* had approximately eight cohorts of leaves present within one tree crown at one point in time, each with varying levels of susceptibility to insect attack. Young leaves that emerged during spring (Oct. – Nov.) were the most preferred by common host-specific beetle larvae that emerged synchronously with flushing; whereas old leaves (> 1 yr) from summer flushes and from the previous year were highly resistant to grazing. In addition, herbivory varied significantly between branches and individual crowns, but not with light regime or height (Selman and Lowman, 1983).

More large-scale comparisons between forest communities are needed to better understand the impact of herbivory as an ecological process. For example, the annual levels of defoliation in Australian tree species ranged from as low as 2-3% in subtropical rain forests to as high as 300% in nearby dry sclerophyll (*Eucalyptus*) stands (Lowman, 1992; Lowman and Heatwole, 1992). Does this imply that one forest is healthier than another? Are different mechanisms regulating insect defoliators and subsequent foliage responses between two forests? Are the trophic structures of herbivores and predators intrinsically different?

The prospect of increased ecological comparisons between and within forests is an incentive to develop better protocols for field sampling of events such as grazing. The process of herbivory has important consequences in forest ecosystems, both economically in terms of pest management and ecologically in terms of maintenance of species diversity. For example, what species are appropriate to sample? Is there greater variation *within* or *between* forests? And how do we tackle these questions with statistical and biological accuracy? And perhaps most importantly in the current urgency of forest conservation issues, can we apply such community level measurements to improve the management and
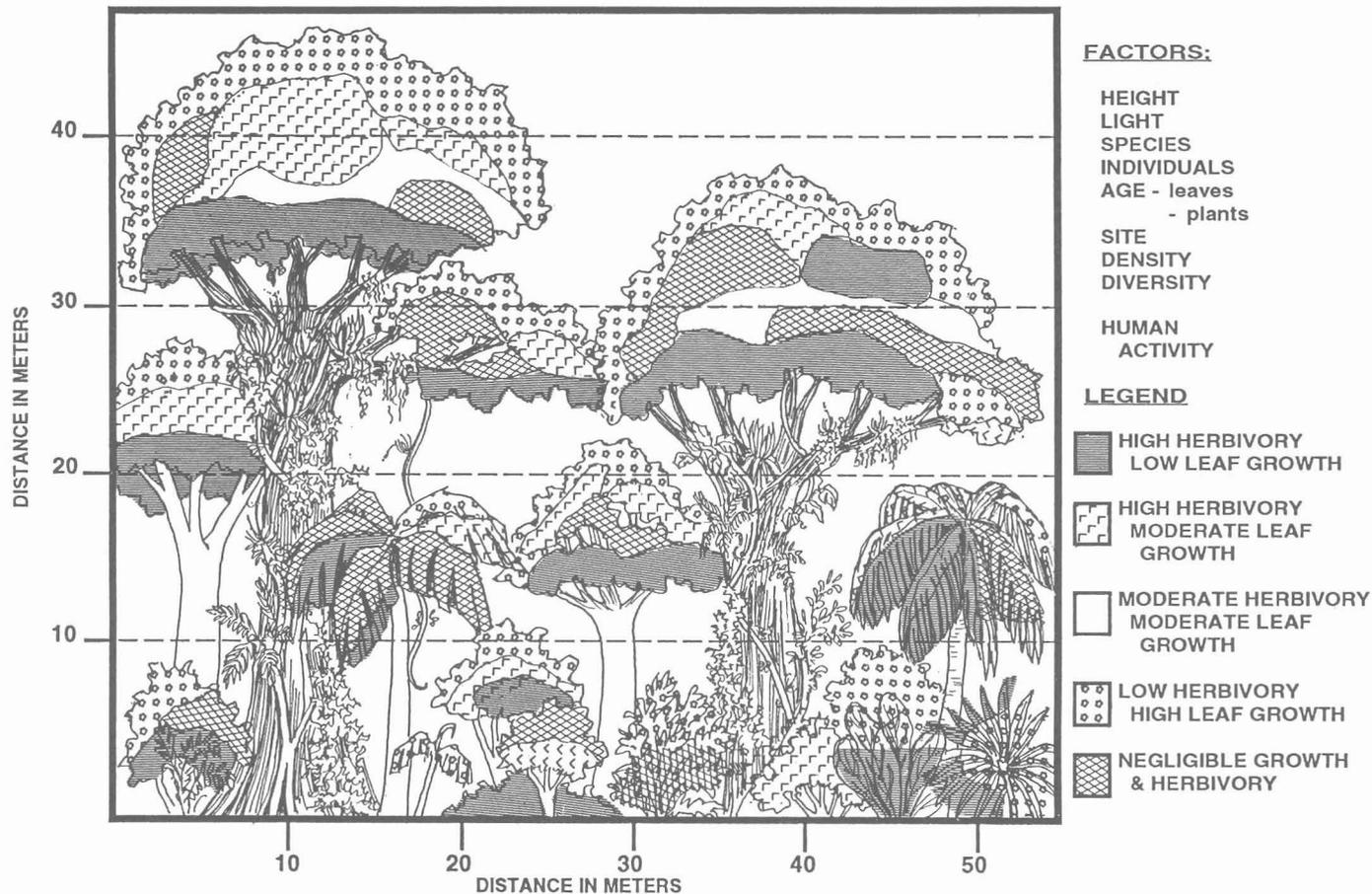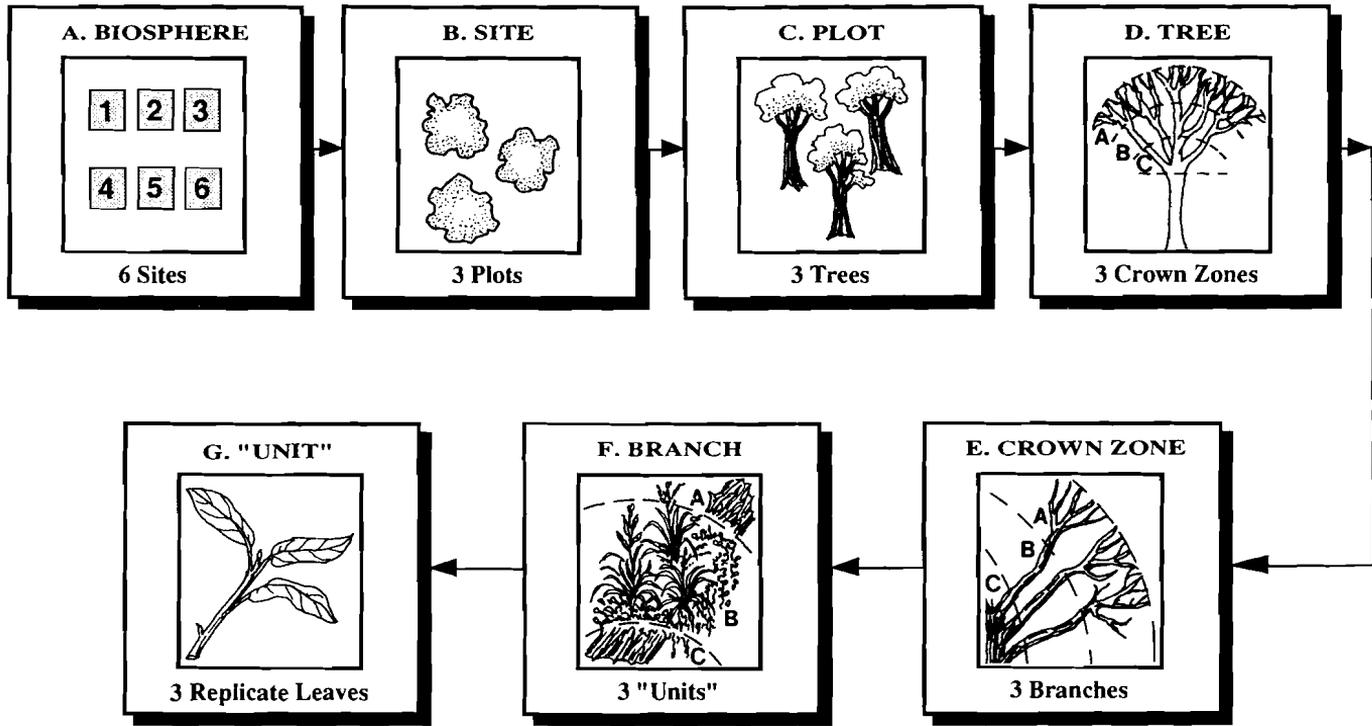
Fig 3. Schematic representation of 'hotspots' in the canopy, where herbivores are attracted to foliage that is more susceptible, and where insect abundance will be highest. 'Hotspots' will vary over time, due to the differences in phenology and foliage qualities among species.

A. BIOSPHERE	B. SITE	C. PLOT	D. TREE
1 2 3 / 4 5 6			A B C
6 Sites	3 Plots	3 Trees	3 Crown Zones

G. "UNIT"	F. BRANCH	E. CROWN ZONE
	A B C	A B C
3 Replicate Leaves	3 "Units"	3 Branches

Sample Design for Canopy Field Work

Fig 4. Experimental design for canopy foliage studies, illustrating the replication recommended at the spatial scales of forest stand, site, plot, tree, crown zone, branch and unit (leaf).

restoration policies in forests that have been altered by human activities or other severe stresses?

Future Directions for Study

I pursued my studies of rain forest herbivory at Sydney University, where I shared office space with the graduate students of Tony Underwood, whose concepts of experimental design on rocky intertidal organisms have greatly improved scientific methods in that ecosystem (e.g. Underwood, 1988). How, I wondered, could one quantify and sample with similar statistical rigour in the canopy? Obviously, the forest canopy has several obvious differences from the rocky intertidal, namely that:

1.   it is extremely three-dimensional with heights of up to 50-60 m (vs. two-dimensional on the rocky shore),
2.   it has organisms ranging a hundred-fold in size e.g., seedlings vs adult trees, thrips vs sloths (in contrast to a more homogeneous range in the intertidal),
3.   it has an air substrate (vs water) that is difficult for human mobility.

The logistics of counting and manipulating herbivores in the forest canopy may be more complicated than on an intertidal rock platform, but the advantages of implementing a sound sampling protocol are enormous.

Different components of a forest canopy must be quantified to measure a specific canopy process. In the case of herbivory, all foliage components plus active herbivores require measurement. Initial observations, using ropes or a platform, are ideal for determining the organisms involved in foliage grazing. It should be emphasized that nocturnal surveys are also important for evaluating herbivore activity. Sampling protocols are illustrated at different spatial scales, ranging from ecosystem to site to individual tree (Fig. 4). All seven spatial scales are important for a thorough ecological understanding of herbivory as a canopy process, although different studies may prefer to approach research at the level of species or of ecosystem.

As habitat destruction continues to reduce the world's forests, canopies will become reduced both in area and in diversity of species. It is predicted that many canopy organisms have already disappeared before they were ever scientifically described, and most of them are presumed to be insects (Erwin, 1982, 1991; Wilson, 1992), including many herbivores. Understanding the maintenance of species diversity in tropical habitats is still an urgent priority (Connell, 1978). The complex interactions between canopy foliage and defoliators is an arena for ecological change as a consequence of human activities. The concept of a forest pest usually implies a foliage-feeding insect and such outbreaks are often the result of human perturbation (e.g., gypsy moth, reviewed by Elkington and Liebold, 1990). Another example is the death of millions of eucalypt trees in Australia, the result of a complex impact of human activities in the rural regions resulting in outbreaks of a scarab beetle (Lowman and Heatwole, 1992). Although pest outbreaks are still regarded as relatively rare events in forests, it is obvious that the natural processes regulating canopy foliage and their defoliators require further study to fully understand the implications of imbalances that result from human impacts.

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