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Herbivory as a Canopy Process in Rain Forest Trees

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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, "Tropical Wild Life" (1917)

I. Introduction

It has long been assumed that forests represented vast expanses of homogeneous green tissue, but this assumption is oversimplified. When walking through a forest, we usually focus our observations on a narrow band of green foliage, from ground level to about 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. Because the majority of plant–herbivore relationships occur where the foliage is located, it is obvious that herbivory as a forest process remains relatively unknown. Fifteen years of observations on herbivory in canopies have given me a different perspective: I no longer see forests as expanses of green, but instead I see them as great mosaics of holes in leaves!

As human beings making observations over relatively short time spans, we usually fail to appreciate the dynamic processes that separate life from death in complex canopy ecosystems. The life of a leaf, which comprises the building block of the forest canopy, is no exception. In a leaf's life span, it

is critical to survive the vulnerable weeks of foliar expansion without being eaten. From a plant's point of view, there exists an evolutionary roulette of rendering one's green foliage less susceptible to successive generations of defoliators. Viewed from the perspective of a herbivore, a complex world of different bites must be recognized: soft versus tough, nutritious versus nonnutritious, old versus young, apparent versus nonapparent, rare versus common, and probably other choices that have not yet been detected by biologists.

Unlike Jack Putz, who can successfully carry out vine studies from his "rocking chair perspective" (Chapter 14), I have been forced to climb into the canopy to study herbivory. Alas, no combination of monkeys, telephoto lenses, helicopters, or low-flying planes offer the quality of detail to substitute for being up there. I have become resigned to a lifetime of aerial exploits, with high hopes (no pun intended) that during my waning years I would be capable of hobbling into the forest to address all my remaining hypotheses on seedlings.

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). The current controversies surrounding the biodiversity of tropical forests have stimulated ecological interest in the numbers of invertebrates in tropical tree crowns (Erwin, 1991; Gaston, 1991; Wilson, 1992). These two topics—insect pests and the biodiversity debate—have fostered a lively literature on herbivory and herbivores in forests, but little research has included the upper crowns.

This review will address the spatial and temporal heterogeneity of herbivory in rain forest tree crowns, with brief coverage of the characterization of their insect herbivore communities. I also emphasize the methodological challenges associated with herbivory as a canopy process, because the reliability of methods has an enormous impact on the accuracy of the results. Studies on understory shrubs and herbs in forests are not included, except where findings are relevant to canopy foliage.

I have also outlined possible protocols for future ecological studies of herbivory as a canopy process. Whereas biologists have successfully counted and measured the abundance of herbivorous mollusks on a two-dimensional system such as intertidal rocky shores (e.g., Underwood and Denley, 1984), the height and structural complexity make it more difficult to count and measure the grazing impacts of invertebrates in a forest canopy. Because of these logistic constraints, biologists have tended to study herbivory in systems other than forest canopies (e.g., Harper, 1977). However, the small number of studies reported here have used canopy access techniques, resulting in a plethora of ecological questions concerning the complexity of arthropod/canopy foliage interactions.

II. Herbivory as a Component of Forest Ecosystems

A. History of Herbivory Studies in Forest Canopies

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 simply phenology with an annual turnover of leaves; (2) measurements were sometimes made from senescent leaves retrieved from the forest floor; and (3) replicated stratified sampling was rarely attempted. In short, defoliation was treated as a discrete, snapshot event (Diamond, 1986), accounting for neither temporal nor spatial variability.

More recent studies have expanded in scope to include temporal and spatial factors to explain heterogeneity of herbivory throughout the canopy. Five noteworthy discoveries in the history of herbivory research are:

1. An important attribute affecting levels of foliage consumption is age of leaf tissue, with soft, young leaves being preferred over old, tough leaves (e.g., Coley, 1983; Lowman, 1985).
2. The most abundant herbivores in forests are insects in terms of both number and estimated impacts (reviewed in Schowalter *et al.*, 1986; Lowman and Moffett, 1993). In some ecosystems, however, mammals are also important, for example, monkeys, koalas, and tree kangaroos (review in Montgomery, 1978).
3. Canopy grazing levels are not homogeneous *between* forests, but range from negligible losses to total foliage losses, and are heterogeneous *within* forests, varying with plant and herbivore species, height, light regime, phenology, age of leaves, and individual crown (e.g., Lowman, 1992).
4. The assumptions common in the 1960s (i.e., that herbivory averaged 5–10% annual leaf area loss and was homogeneous throughout forests) were oversimplified and underestimated, particularly for evergreen forests (e.g., Fox and Morrow, 1983).
5. Foliage feeders are featured in the ecological literature as the most common type of herbivore. However, sap-suckers may also be important although they have not been as well studied. Foliage consumption is reputedly easier to measure than sap consumption, yet even for measurement of folivory, standard protocols are not well established (see Lowman, 1984b).

During the 1980s, canopy access was developed, which expanded the scope of foliage sampling, and studies of herbivory in evergreen tropical forests subsequently increased.
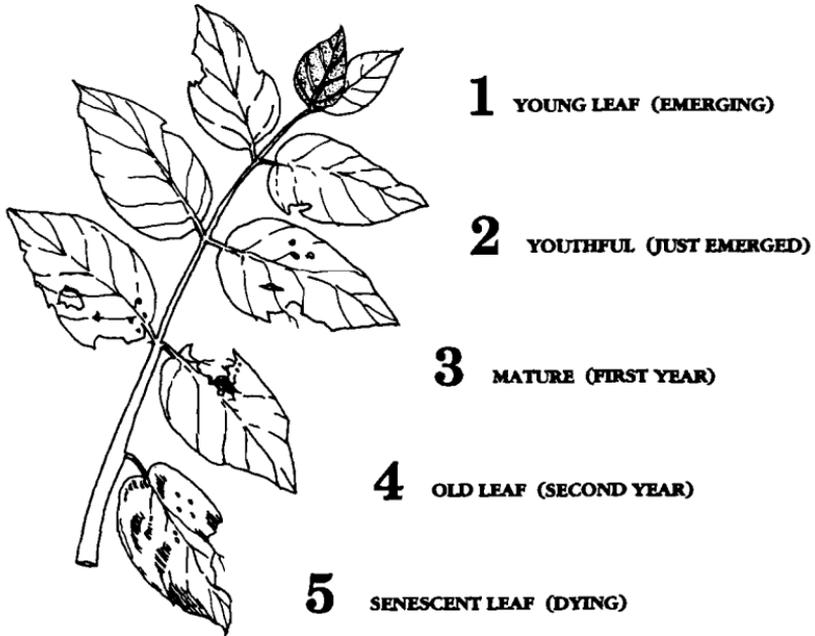
B. Role of Herbivory in Canopy Processes

The consumption of plant material by herbivores is a subject of great economic and ecological importance (e.g., Barbosa and Schultz, 1987; Price *et al.*, 1991). Because forest canopies contain the bulk of terrestrial photosynthetic material that is involved in the production of oxygen and maintenance of global biogeochemical cycles (review in Wilson, 1992), the processes affecting canopy foliage have direct consequences on the health of our planet. Leaf predation is an example of such a process. The loss of foliage by predators can occur by direct consumption or by less obvious impacts such as mining, sap-sucking, and leaf-tying. Herbivory affects foliage during almost all stages in the life of a leaf, and leaves have subsequently become adapted with defenses against predation (Fig. 1). Levels of herbivory range from negligible grazing to the mortality of leaves, branches, entire crowns, and sometimes whole forest stands.

The study of herbivory as an integrated process throughout a forest stand requires information on many aspects of forest biology, including plant phenology, demography of insect populations, leaf growth dynamics, tree architecture, foliage quality, physical environment, nutrient cycling, and plant succession. Recent interest in plant–insect relationships has emphasized single-species relationships with fewer investigations at the ecosystem level. It has also centered around studies of shrubs and herbs. Few studies of trees exist, with even fewer that involve entire forest stands and almost none that includes the canopy. Ironically, forest canopies comprise an ecological arena where plant–insect relationships may be most complex in terms of spatial, taxonomic, temporal, structural, or any other measurable factor.

Herbivory is an ecological process that affects all canopy components (Fig. 2), either directly or indirectly. Foliage is removed directly by herbivores (called "primary consumption") or else it escapes, resulting in "secondary consumption," whereby foliage senesces and then decomposes via arthropods on the forest floor. Both fates comprise pathways that link herbivory to nutrient cycling in the forest ecosystem, either via frass or via leaf litter. Foliage that is partially grazed by herbivores is called "herbivory," whereas foliage that is grazed in entirety (or grazed extensively and then senesces) is classified as "defoliated." It is important to recognize that herbivory is the direct effect of grazing, whereas defoliation results in mortality that may only be partially a consequence of the grazing mechanism.

Herbivore populations fluctuate in the canopy and in turn affect the populations of other invertebrates and of birds and mammals that feed

1 YOUNG LEAF (EMERGING)

2 YOUTHFUL (JUST EMERGED)

3 MATURE (FIRST YEAR)

4 OLD LEAF (SECOND YEAR)

5 SENESCENT LEAF (DYING)

age class	POTENTIAL FACTORS OF MORTALITY	MECHANISMS OF PROTECTION
1.	Desiccation	Morphology, phenology
	Herbivory	Morphology, phenology, chemistry
	Physical Damage	Morphology, phenology
2.	Desiccation	Morphology, phenology
	Herbivory	Morphology, phenology, chemistry
	Physical Damage	Morphology, phenology
3.	Herbivory	Morphology, phenology, chemistry
	Physical Damage	Morphology, phenology
4.	Herbivory	Morphology, phenology, chemistry
	Epiphylly	Morphology, chemistry
5.	Decay	Morphology, phenology, chemistry
	Age	

Figure 1 Leaf age classes as defined for use in rain forest canopy growth and herbivory studies, with factors affecting survival at each stage.

on these herbivorous organisms (e.g., Woinarski and Cullen, 1984). Even stand growth and dynamics may be ultimately affected by herbivory, and by the susceptibility of a species to grazing (review in Schowalter *et al.*, 1986). The impact of leaf consumption on herbs, seedlings, and shrubs has been quantified in terms of mortality, succession, and compensatory growth (e.g., Lowman, 1982; Coley, 1983; Marquis, 1991). Such factors are more
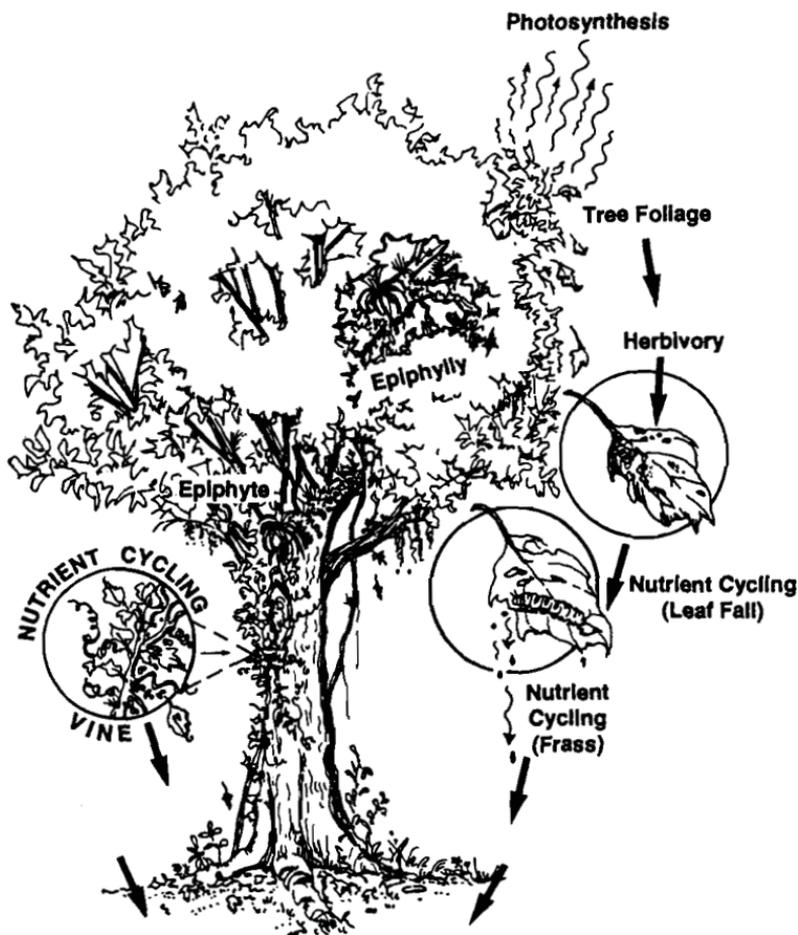
Figure 2 Canopy components and processes that are affected by herbivory in a forest stand.

difficult to measure for tall trees and across entire forest stands. Examples of herbivory that have been integrated with other aspects of forest dynamics include studies on the spatial distribution of canopy insect populations in the Australian rain forest tree *Argyrodendron actinophyllum* (Basset, 1991), nutrient cycling via frass or litterfall pathways (Lowman, 1988), pest outbreaks and stand mortality (e.g., Lowman and Heatwole, 1992), and herbivory in relation to phenology of stands (Schultz and Baldwin, 1982).

III. Canopy Foliage and Estimates of Its Defoliation

In many temperate forests and some seasonal tropical forests, annual and cumulative herbivory are the same: every year, a full cohort of leaves

emerges and senesces (Kikuzawa, 1983). Herbivory in evergreen forest canopies may be more complicated, because the cycles of leaf turnover are not always seasonally distinct (e.g., Lowman, 1992). Consequently, ecologists in these habitats are confronted with many cohorts or leaf populations within one crown, requiring a more complex sampling design to ascertain both annual defoliation and cumulative herbivory over a leaf's life span.

In evergreen forests, leaf longevity is extremely variable, and the canopy is a complex mosaic of different-aged leaves, with different susceptibilities to herbivores. Evergreen rain forest leaves have life spans ranging 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).

In recent years, the complex temporal and spatial patterns of leaves 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 (reviews in Lowman, 1984b; Landsberg 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 year) 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).

Herbivory in canopies ranges from negligible (e.g., Schowalter *et al.,* 1981; Ohmart *et al.,* 1983) to over 300% of annual foliage production in cases where eucalypts refoliated three successive times after defoliation (Lowman and Heatwole, 1992). The comparison of herbivory measurements from several forest canopies presented in the following illustrates the variability in levels of defoliation *between* forest types, although the different methods employed may be a source of some of the apparent variation (Table I).

Herbivory levels vary significantly both between species and between forest types, as illustrated by my long-term studies in Australian rain forests (Fig. 3). I originally hypothesized that evergreen forests with lower diversity would have higher herbivory than neighboring evergreen forests with higher diversity (Lowman, 1982). The cool temperate rain forest, where *Nothofagus moorei* dominated over 75% of the canopy, averaged an annual 26% leaf area loss to grazing insects (Selman and Lowman, 1983). The majority of that was due to a host-specific chrysomelid beetle that fed

Table I Studies of Herbivory in Forests (Including Understory)

Location	Forest type	Level of grazing	Technique[a]	Source
Costa Rica	Tropical forest	7.5% (new leaves)	1	Stanton (1975)
	Tropical evergreen	30% (old)	1	
Panama	Tropical evergreen	13%	1	Wint (1983)
Panama (BCI)	Tropical evergreen	8% (6% insect;		
		1–2% vertebrates)	2,5	Leigh and Smythe (1978)
		15%	2,5	Leigh and Windsor (1982)
	Understory only	21% (but up to 190%)	3	Coley (1983)
Puerto Rico	Tropical evergreen	7.8%	2	Odum and Ruiz Reyes (1970)
		5.5–16.1%	4	Benedict (1976)
		2–5%	4	Schowalter (1994)
New Guinea	Tropical evergreen	9–12%	1	Wint (1983)
Australia	Montane or cloud	26%	4	Lowman (1984b)
	Warm temperate	22%	4	Lowman (1984b)
	Subtropical	14.6%	4	Lowman (1984b)
Africa–Cameroon	Tropical evergreen	8–12%	4	Lowman (1993)
North America	Temperate deciduous	7–10%	1	Bray (1961)
	Temperate deciduous	1–5%	4	Schowalter et al. (1981)
	Coniferous	<1%	7	Schowalter (1989)
Australia	Evergreen	15–300%	4	Lowman and Heatwole (1992)
	Dry	11–60%	1	Fox and Morrow (1983)
		3–6%	6	Ohmart et al. (1983)
Europe	Deciduous	7–10%	1	Nielson (1978)

[a] 1, Visual ranking; 2, litter trap; 3, graph paper or template squares; 4, LA meter; 5, other calculations; 6, insect frass; 7, estimation of missing or truncated needles.
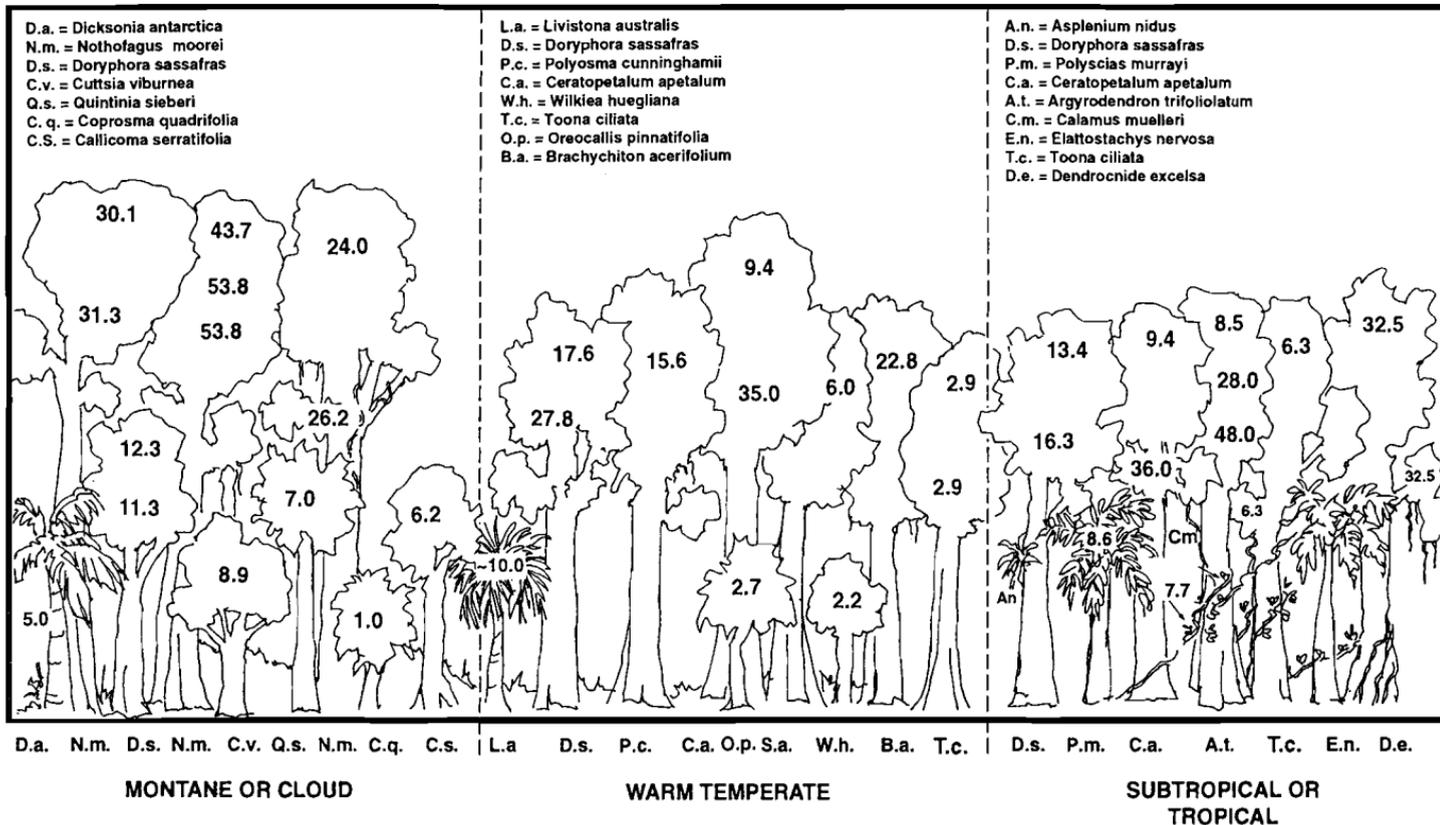
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Figure 3 Variation in herbivory between species, heights, and sites along an elevational gradient in Australia.
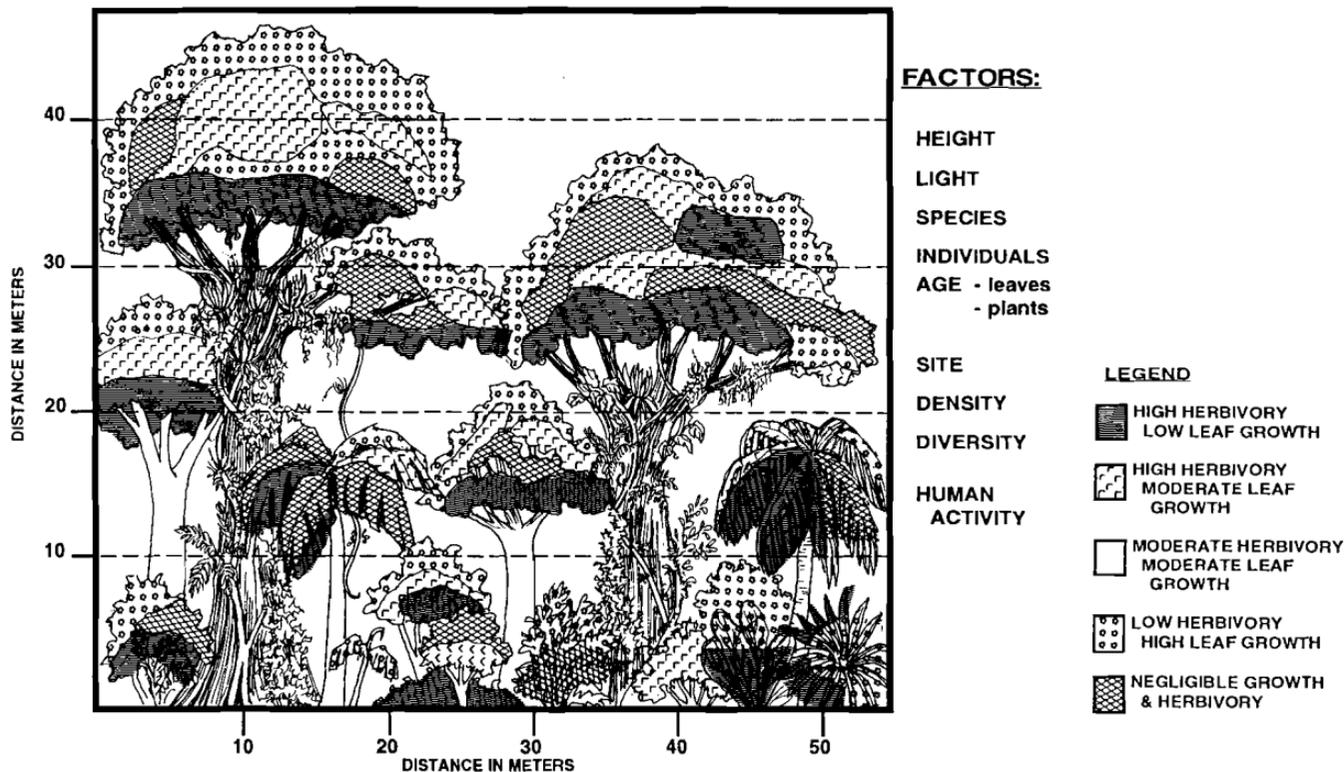
Figure 4 Schematic representation of "hot spots" in the canopy, where herbivores are attracted to foliage that is more susceptible. It should be possible to sample for insect herbivores in specific regions of the canopy rather than throughout this complex array of foliage. "Hot spots" will vary over time, due to the differences in phenology and foliage qualities among species.

exclusively on the young leaves of *N. moorei* during the spring flush. In contrast, the subtropical rain forests, where no species occupied more than 5% of the canopy within a stand (Lowman, 1985), averaged only 15% annual leaf area losses to insect grazers. Herbivory also varied significantly among species. *Toona australis* (Meliaceae), which is relatively rare and is annually deciduous, averaged <5% losses, whereas neighboring canopies of *Dendrocnide excelsa* (Urticaceae) that colonize gaps averaged over 40% annual leaf area losses (Lowman, 1992).

In addition to variation in grazing levels between species and stands, herbivory is variable within individual crowns. 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 long-term studies, I was able to pinpoint "hot spots" in the canopy where grazing will be predictably higher (Fig. 4). These "hot spots" included areas of predictable 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 attracted more insects due to the presence of flowers, epiphytes, or vines (e.g., Lowman, 1992; Lowman *et al.*, 1993b).

For example, long-term measurements of *Nothofagus moorei* showed that crowns exhibited different grazing levels with leaf age, different stands, and time (Selman and Lowman, 1983). *Nothofagus moorei* had approximately eight cohorts of leaves present in the canopy at one point in time (Fig. 5), each with varying levels of susceptibility to insect attack. Young leaves that emerged during spring (Oct.–Nov.) were the most preferred by the beetle larvae who emerged synchronously with flushing, whereas old leaves (>1 year) 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 comparisons between forests are needed to better understand the impact of herbivory on forests. For example, the annual levels of defoliation in Australian trees ranged from as low as 8–15% in subtropical rain forests to as high as 300% in nearby dry sclerophyll (*Eucalyptus*) stands (Lowman, 1992; Lowman and Heatwole, 1992). In this case, different mechanisms are clearly regulating insect defoliators and subsequent foliage responses in two forests. Gentry cited the need for comparisons between Central and South American forests as the stimulus for a recent Association for Tropical Biology symposium and the subsequent production of a volume on four neotropical forests (see Gentry, 1990). Similarly, a recent American Institute of Biological Sciences session was held to stimulate comparisons between
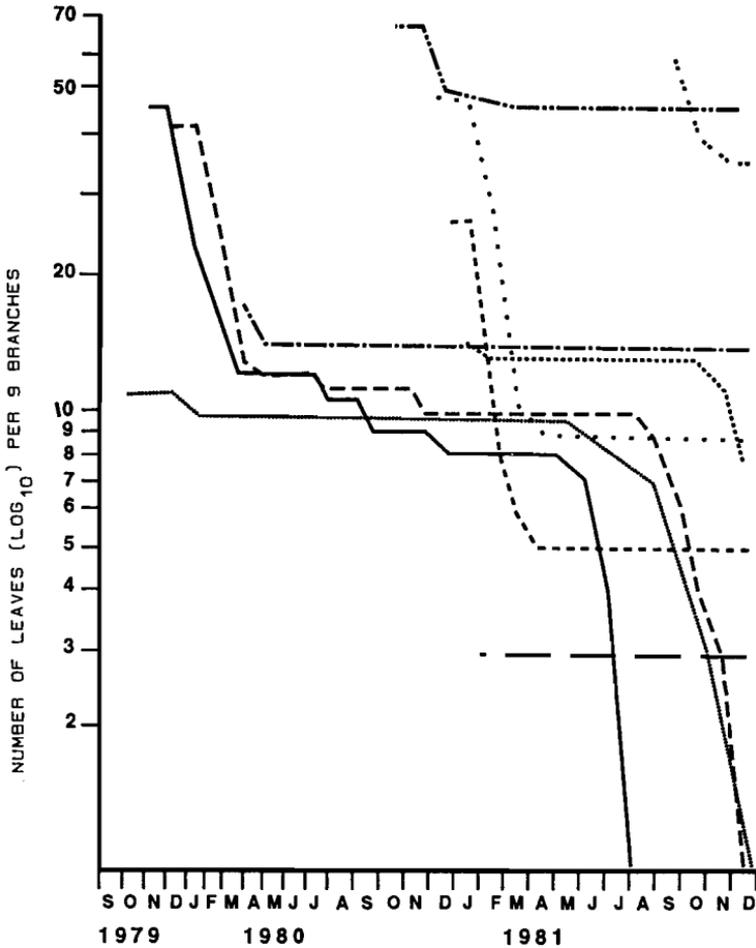
Figure 5   Leaf survivorship curves for leaves of *Nothofagus moorei* (Fagaceae) in cool temperate rain forests of Australia that flushed during a 2-year period (September 1979–September 1981) expressed on a Log_{10} scale. Leaves were tallied from nine branches and illustrate the complexity of cohorts throughout the canopy of a tree that exhibits a bimodal seasonal flush.

Neotropical and Paleotropical forests (Lowman, 1993). The prospect of increased ecological comparisons between forests is an incentive to develop better protocols for field sampling of events such as grazing. 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?

IV. Dynamics of Herbivores in Forest Canopies

Although mammals are obviously important herbivores in grasslands and other ecosystems, there is relatively little research on the impacts of mammals grazing in forest canopies. Koalas, tree kangaroos, sloths, birds, monkeys, and porcupines are some of the well-known herbivorous mammals that frequent the canopy (review in Montgomery, 1978). In this chapter, insects remain the focus, because their role as herbivores is purportedly more widespread throughout forests. More information on canopy mammals is available in Chapters 10 and 11.

A. Patterns of Distribution and Abundance of Insect Herbivores in the Canopy

In a classic study, Southwood (1961) examined the species of insects in tree canopies in Great Britain. For several species of temperate deciduous trees, he found that more diversity was associated with trees that had been established over a long time period as compared to species introduced more recently. His insecticidal knockdown procedure has since been altered to include "misting" (Kitching *et al.*, 1993), "fogging" (Erwin, 1982), and "restricted canopy fogging" (Basset, 1992), as more biologists become curious about the variety and numbers of insects in tree canopies. Similar to the artifacts of sampling for foliage consumption measurements, the variability in methodology to assess the diversity of insects in trees also leads to discrepancies in our estimates of herbivorous insects.

Just how many insects are found in tree canopies, and what proportions are herbivorous? (This topic is reviewed more comprehensively in Chapter 5.) Over the past 15 years, the hypothesized numbers of species of arthropods in trees has expanded from 1–2 million (Southwood, 1978) to far higher estimates of 8–10 million (Adis, 1990), 10–30 million (Erwin, 1982, 1991), and as high as 100 million (Wilson, 1992), of which just under 50% of insect species classified are reputed to be herbivorous (Wilson, 1992). From these predictions, one can speculate that as many as 49 million herbivore species may exist!

The major contributions to our knowledge of the canopy herbivore community have been extrapolations using ground-based studies of saplings and shrubs. It is obvious that woody plants sustain more insect species than herbaceous species, although few studies have quantified these differences (but see Basset and Burckhardt, 1992). In herbaceous plants, hosts with greater chemical complexity appear to support herbivores with higher degrees of specificity (Berenbaum, 1981). Will canopy trees show similar patterns to herbs? Seedlings of a Neotropical tree with high tannin concentrations sustained lower herbivory levels than seedlings with low tannin levels

(Coley, 1986), but can we extrapolate from seedlings to adult trees? It is daunting to design a rigorous sampling regime that would replicate within and among tall trees; but as canopy access becomes easier, the opportunities for this work may arise.

Herbivores, as with other invertebrate groups, are assumed to attain higher diversity in tropical forest canopies, with progressive decreases in temperate forests (e.g., Kitching *et al.,* 1993). Four hypotheses are posed to explain this population decline away from the equator. These are: (1) historical—higher latitudes are out of equilibrium due to recent glaciation (Wallace, 1878); (2) structural—the tropical environment contains more niches (MacArthur and MacArthur, 1961); (3) dynamic—predation and competition in the tropics permit more species to coexist (Janzen, 1970; Connell, 1978); and (4) energetic—the higher stability of productivity in the tropics permits greater specialization within ecological niches (Connell and Orians, 1964). In canopies, more data are required to test hypotheses to explain the underlying reasons for the distribution of insect herbivores.

The density of herbivores in the canopy might be predicted to be higher in the upper crown where new foliage is relatively more abundant, as insects prefer to feed on young foliage (Coley, 1983; Lowman, 1985). However, herbivores also aggregate in the lower shade regions of crowns during leaf-flushing periods (Lowman, 1985). The methodological problems associated with quantifying such densities of small, numerous organisms are enormous. Basset *et al.* (1992), using branch-clipping techniques, obtained three times higher arthropod densities in the canopy than in the shrub layer of a lowland rain forest in Cameroon. In a geographical comparison, they obtained 20 arthropods per m^2 in tropical foliage as compared to a range of 19–78 herbivores per m^2 in temperate trees (Basset and Burckhardt, 1992) and 11 herbivores per m^2 in a subtropical tree (Basset and Arthrington, 1992). As predicted by Elton (1973), densities of arthropods may be higher in temperate than in tropical canopies, but only during peaks such as in midsummer.

In temperate deciduous forest canopies, the abundance of invertebrates was found to be higher near ground (0–2 m) than in the canopy (>20 m) (Lowman *et al.,* 1993a), probably due to the increase in the number of niches and more favorable microclimate nearer to the ground. This pattern is reversed in the tropics (Erwin, 1982; and Chapter 5).

Homoptera are a relatively well-studied group of herbivores, but even their abundance is difficult to interpret. Using nets, Elton (1973) measured a density of 0.044–0.078 Homoptera per m^2 ground surface, whereas Wolda (1979), by fogging at 0–16 m, measured 3.5–11.8 Homoptera per m^2 of ground surface. Wolda also found more Homoptera in a canopy with

vines as compared to canopy trees without vines, and he suggested that the more complex canopy architecture may support more insects.

In initial results of a long-term fogging analysis in Australian rain forests, proportions of herbivorous groups (of the total invertebrate catch) were 25% in tropical forest, 13% in subtropical forest, and 23% in cool temperate forest (Kitching *et al.,* 1993). In dry sclerophyll forest canopies, pest outbreaks occur with greater frequency, leading to greater fluctuations in insect numbers. For example, during an outbreak of psyllids, herbivores comprised as high as 71.3% of the total catch (Majer and Recher, 1988). The next decade of research, with improvements in the field techniques and analyses of canopy insects, should bring a better understanding of the distribution of herbivores in tree crowns.

B. Crown Phenology and Stand Dynamics in Relation to Herbivores

The seasonality of growth in the canopy is critical to the process of herbivory. Leaves in tree crowns are more susceptible to being eaten when they are young, soft, situated lower in the crown, grown in shade conditions of the lower canopy, and of a mesophyllous, pioneering species as compared to a sclerophyllous, climax species (Coley, 1983; Lowman, 1985). For herbivores, the availability of evergreen, continuously flushing foliage differs from that of deciduous or intermittently flushing crowns.

In the canopies of five Australian rain forest tree species, I found that most defoliators fed as part of a guild, that is, several insect species were repeatedly observed eating leaves of several neighboring tree species, but they concentrated on leaves of similar phenology comprising the same age and texture of leaf tissue (Lowman, 1985). Similar to Basset's (1992) results on booyong trees, I found few herbivores exhibiting host specificity. However, those that did specialize consumed large amounts of foliage on their host tree. For example, a chrysomelid beetle (*Novocastria nothofagi* Selman) annually consumed >50% of the new leaves of *Nothofagus moorei* (Fagaceae). The beetle larvae emerged synchronously in spring with the annual flush of this beech. *Nothofagus moorei* leaves live for 2 years; consequently, annual spring leaf flushes of beech replace half of the canopy each year in this montane or cool temperate rain forest canopy tree (Fig. 5). Because *N. moorei* grows in single-species stands, the beetle's host-specific behavior has a significant impact on the canopy in this ecosystem. No canopy trees were observed to die from defoliation during 15 years of study, although this is too short a duration in the lifetime of a tree that reputedly persists for many hundreds of years.

In summary, a growing body of literature on forest insects makes it possible to predict regions of higher diversity or "hot spots" of arthropods in the canopy, namely, forests situated in the tropics, young leaves, single-

species stands, shade leaves in the lower canopy with their softer texture and lower toxicity, and pioneering species with soft leaves.

C. Feeding Behavior of Herbivores in Tree Crowns

Much has changed since Hairston *et al.* (1960) claimed that green foliage was equally available to herbivores, and that the impact of insects on forests was negligible. Research on the relationships between insects and foliage has expanded into chemistry, phenology, seasonality, species, succession, age of leaf tissues, toughness, and a multitude of factors—in short, the green world is complex!

Despite the enormous numbers of forest Lepidoptera (over 120,000 species described worldwide), fewer than 15 species have been documented as causing outbreaks (Mason, 1987). Insect outbreaks are most frequently associated with temperate forests, probably because their economic impacts are more closely monitored (although intermittent accounts in the literature attest to the existence of pest epidemics in tropical forests; e.g., Wolda and Foster, 1978; Selman and Lowman, 1983; Wong *et al.,* 1991). Foliage loss during outbreaks can reach 100% defoliation (reviewed in Schowalter *et al.,* 1986) or even 300% annually in evergreen species such as *Eucalyptus* that repeatedly undergo reflushing of their canopies after defoliation (Lowman and Heatwole, 1992).

In his classic studies, Janzen (1970) suggested that high levels of host specificity exist in tropical plant–insect relationships, but his assumptions were primarily based on observations of seed predators. In later reports, he found that the majority of caterpillars in a Costa Rican deciduous forest were monophagous (Janzen, 1988). Of the few studies of the host specificity of other herbivores in tropical tree canopies, lower levels of host specificity were observed. Erwin (1982) found 20% host specificity in Coleoptera in *Luehea seemanii* in Panama. In his comprehensive studies of the invertebrates of *Argyrodendron actinophyllum* in Australian subtropical rain forest, Basset found only 11% host-specific herbivores (1992), results similar to earlier collections on five Australian canopy trees (Lowman, 1985). Of the relatively few lepidopteran defoliators on Asian dipterocarps, most were polyphagous (Holloway, 1989). There is still too little information to fully explain the feeding behavior of herbivores in trees.

Few data exist on other types of herbivores such as miners and sapsuckers. Approximately 31 mines per m^2 leaf area were calculated for a subtropical canopy tree (Basset, 1991), whereas less than 2% of leaves in nearby dry sclerophyll canopies contained any galls (Lowman and Heatwole, 1992). Although the impact of foliage feeders may be directly measured in terms of leaf area lost, the damage to a tree from mining or sapsucking is less apparent without detailed physiological studies.

V. Impact of Ecological Methods on Our Assessment of Herbivory

A. Methods to Measure Herbivory: Are They Accurate?

The turnover of photosynthetic tissue not only has direct impact on the growth and maintenance of the trees, vines, epiphytes, and herb layers of the forest, but the production of green tissue is indirectly responsible for the maintenance of all animal life in the canopy. The ability of biologists to measure foliage and predict photosynthetic activity in forests has become an important topic in advocating the conservation of forests. It is obviously important to make accurate measurements of both the production of foliage in a forest and of the removal of leaf material by herbivores in order to assess forest productivity.

The methods used to measure herbivory have direct consequence on our understanding of herbivore dynamics. As biologists historically became interested in defoliation, a plethora of literature on herbivory was produced, much of which utilized different (and not entirely comparable) methods. For example, the techniques used to measure foliage losses include visual estimates (e.g., Wint, 1983), graph paper tracings (Lowman, 1984b), templates in the field (Coley, 1983), and leaf area meters (Lowman, 1984b). Similarly, the sampling designs varied, including leaves collected in litter traps (Odum and Ruiz-Reyes, 1970), leaf selection undefined (Bray, 1961), leaves marked in the understory (Coley, 1983) and upperstory (Lowman, 1985), leaves marked along a vertical transect (Lowman, 1992), and frass collections (Ohmart *et al.*, 1983). Obviously, such sampling designs may be adequate for the particular hypothesis they address, but they are not conducive to intersite comparisons (e.g., Lowman, 1987). In some cases, literature reviews have misquoted herbivory levels, perhaps because it is so difficult to interpret the various methods employed by different studies (e.g., Landsberg and Ohmart, 1989).

Comparison of discrete versus long-term measurement techniques in rain forest canopies revealed discrepancies of up to fivefold, with long-term studies producing significantly higher measurements. For example, estimates of herbivory levels in Neotropical saplings were three times higher than in previous studies that used discrete, harvested leaves (21% in Coley, 1983, versus 7% in Odum and Ruiz-Reyes, 1970). Similarly, long-term measurements of coral cay shrubs produced estimates of 21% area missing (Heatwole *et al.*, 1981) compared to levels of 2–3% measured by discrete sampling (Lowman, 1984a). Grazing in some plant communities may be higher than recorded previously from discrete measurements of missing-leaf area, which results in an underestimation of the impact of herbivory. Temporal variability in levels of herbivory further complicates our ability to monitor this canopy process.

In addition to the potential errors from methods that do not account for heterogeneity of foliage throughout the canopy, other methods must be used with caution. Daily rates of defoliation are useful but can be misleading if measured only over short durations, as they will not account for seasonal differences. The use of grazing categories (e.g., ranking 1–5) are useful for quick, rapid assessment, but such information may not be transformable into numbers that can be statistically tested. And the assumption that the presence of leaf petioles indicates 100% defoliation may be misleading, because physical factors are also responsible for loss of a leaf blade. The extent to which methods may alter results remains a critical issue in the literature on herbivory.

B. Possible Protocols for Future Sampling

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. How, I wondered, could one quantify and sample with similar statistical rigor in the canopy? Obviously, the forest canopy has several obvious differences from the rocky intertidal, namely:

1. it is extremely three dimensional with heights of up to 50–60 m (versus two dimensional on the rocky shore);
2. it has organisms ranging a 100-fold in size, for example, seedlings and adult trees, thrips and sloths (versus a more homogeneous range); and
3. it has an air substrate (versus 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 (Fig. 1) 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 (Fig. 6) to site (Fig. 7) to individual tree (Fig. 8). At least seven spatial scales (Fig. 6) 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.

During 13 years of canopy research in Australia, I developed protocols for measuring herbivory in rain forest tree canopies, using replicate sites, trees, canopy heights, branches, and leaves. In the subtropical hammocks
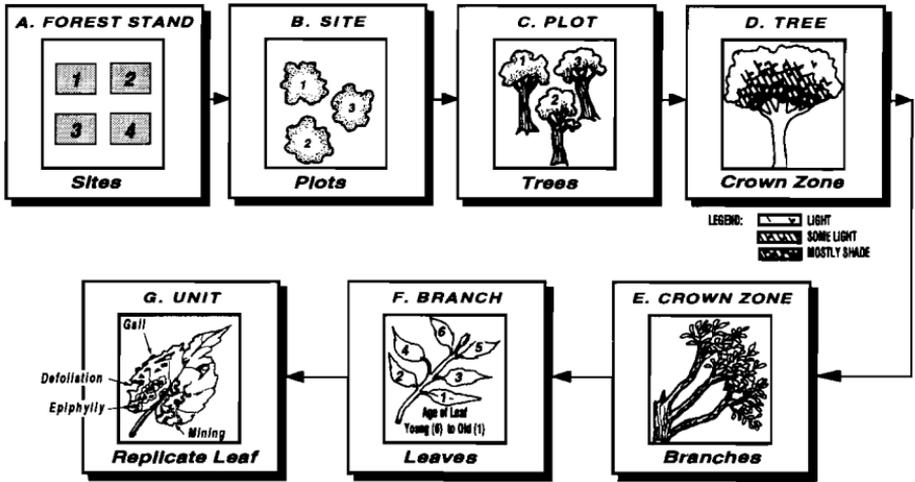
Figure 6   Experimental design for canopy foliage studies, illustrating the replication recommended at the spatial scales of forest stand, site, plot, tree, crown zone, branch, and unit (leaf).

of Florida, a group from The Marie Selby Botanical Gardens is currently working out protocols to measure herbivory and growth dynamics of vines and epiphytes. The ideal replication for ecological sampling in the canopy involves spatial replication (Fig. 6) with a temporal component (Fig. 1). Monthly sampling is ideal for herbivory studies, with weekly or daily measurements during periods of active leaf flushing and flowering. Because this
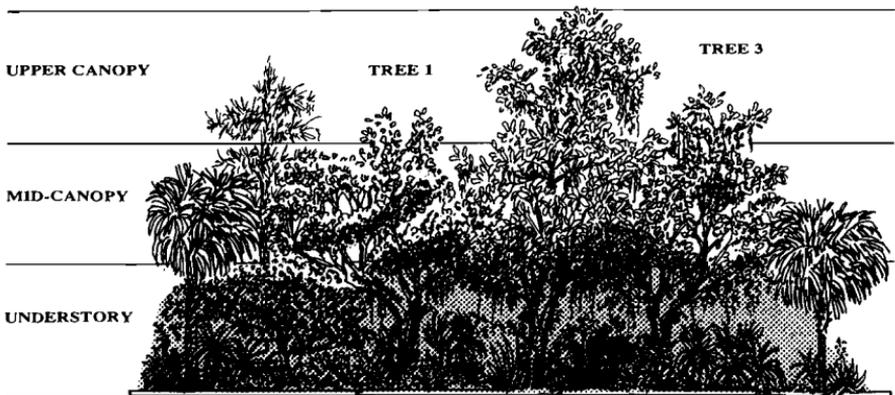

Figure 7   Generalized subtropical oak–pine hammock site regime for canopy foliage studies, illustrating the structural regions of understory, midcanopy, and upper canopy that vary in light levels and other microclimatic factors. Shade leaves are indicated by gray shading, and sun leaves are shown in white.
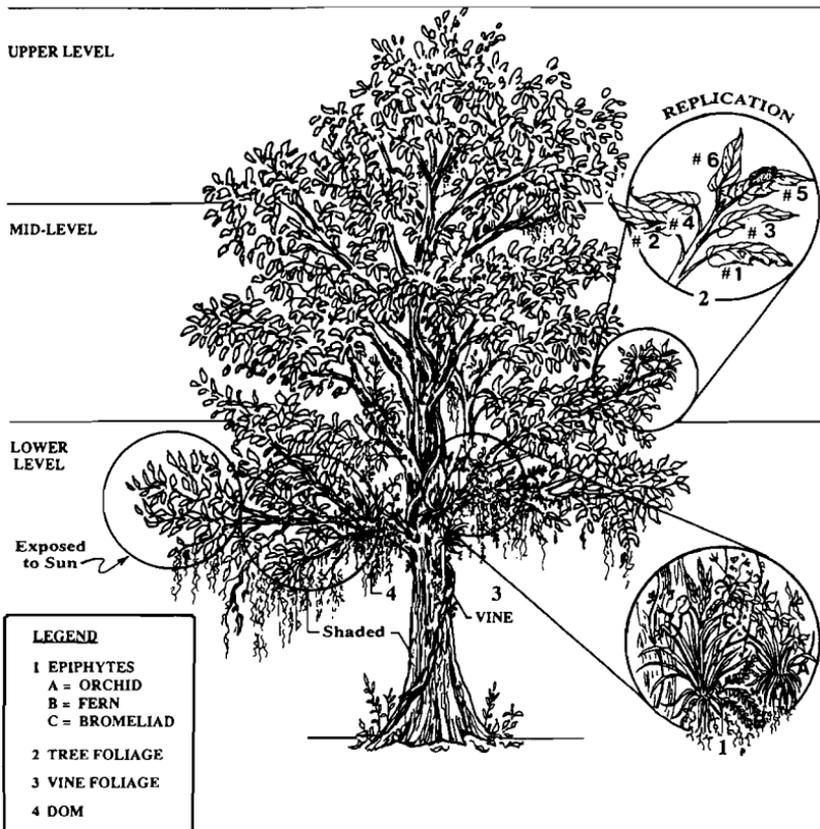
Figure 8 Schematic diagram of the components of a forest canopy to sample, including epiphytes (orchid, fern, and bromeliad), tree foliage, vines, and DOM (dead organic matter).

frequency of sampling is not possible for most studies that are situated in remote sites, techniques that are more rapid and time-efficient must be developed, as with most ecological studies involving dynamic interactions.

VI. Conservation of Forest Canopies and Future Implications of Herbivory as an Ecological Process

As habitat destruction continues to reduce the world's forests, canopies will become reduced both in area and in diversity of species. It is believed that many canopy organisms have already disappeared before they were

ever scientifically described. Most of them are presumed to be insects (Wilson, 1992), including many herbivores. 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 denotes 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.

Long-term studies and quantified maps of herbivore distributions and of the patchiness of herbivory in tree canopies are needed. Some of the many unanswered questions in canopy foliage–insect interactions include:

1. How do spatial and temporal factors affect the distribution of insect herbivores throughout the canopy—both *within* and *between* different tree crowns?
2. What is the variation in levels of herbivory over longer time scales in canopies?
3. How does stand diversity in forests affect the feeding patterns of herbivores?
4. What are the small-scale and large-scale consequences of patchy herbivore attack within one region of an individual canopy?
5. What is the trophic structure of canopy insects?
6. Ultimately, what effect does herbivory have on other processes such as photosynthesis and nutrient cycling in the canopy? Does it influence succession?

Herbivores and the process of herbivory are a complex and integral component of the forest ecosystem. In the tropics, the opportunities to study these ecological interactions under natural conditions are becoming more reduced, as human beings increasingly destroy and alter tropical forests. However, studies of insect pests in disturbed or regenerating forests will become more commonplace. In *The Lorax* (1971, Random House), Dr. Seuss presented the potential problems concerning loss of forests and their canopy inhabitants, and suggested a solution,

Plant a new Truffula. Treat it with care.
Give it clean water. And feed it fresh air.
Grow a forest. Protect it from axes that hack.
Then the Lorax and all of his friends may come back. . . .

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