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# Herbivory in Australian Rain Forests, with Particular Reference to the Canopies of *Doryphora sassafras* (Monimiaceae)

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## ABSTRACT

Herbivory in the canopies of Australian rain forest trees was measured from 1979–1988, and their associated leaf growth dynamics quantified. Levels of defoliation were compared on several spatial scales: within and among canopies of one species (*Doryphora sassafras* Endl.) (Monimiaceae), between species, and among sites, light, and height. Sassafras was distributed throughout all rain forest formations in New South Wales, from the upper elevation cool temperate sites to the warm temperate and lowland subtropical sites. In addition, two methods of measuring herbivory were compared. One method (long-term observations) measured losses up to four times greater than estimates obtained by the second and more conventional technique of harvesting leaves to measure missing surface areas (discrete sampling). Leaf area losses in Australian rain forests averaged between 14.6 percent and 27 percent, ranging from 3.3 percent to 41 percent with species and site. The factors contributing to this variability within Australian forests and compared to studies elsewhere are discussed.

*Key words:* *Australia;* Dotyphora; *herbivory; leaf area; leaf growth; rain forest; tropics; patchiness.*

The resource availability of green foliage for herbivores in forests appears enormous, particularly in rain forests, with their tall trees and multilayered canopies. But, while it is clear that different tree species differ in quality of resource for herbivores and in herbivory rates (*e.g.*, Coley 1982, Lowman 1986b), the variation in both availability and utilization of this resource within and among canopies of different rain forest trees has not been quantified other than by general, short-term surveys (*e.g.*, Odum & Ruiz-Reyes 1970, Leigh & Windsor 1982, Proctor *et al.* 1983). Most studies have involved the discrete harvest of lower canopy leaf samples and subsequent measurement of missing surface area, a fairly simplistic approach to a complex interaction. The variability of biological and environmental conditions throughout the complex vertical distribution of rain forest foliage may affect leaf palatability. These factors include light, height, aspect of canopy region, age, species of tree, elevation, and other site-related characteristics. Some of these factors (*e.g.*, height, light, species) may also act as constraints to the distribution of herbivores.

In this study, spatial and temporal factors affecting herbivory and related leaf growth dynamics were quantified over ten years, a relatively long-term study in scientific terms, albeit short in terms of rain forest phenology. Several questions were addressed, in particular: How is the apparent vast green resource of leaves partitioned among herbivores? What factors contribute to the patchiness in herbivory of one species in particular (*D. sassafras*) both within and among different Australian rain forest canopies?

My results indicate that general surveys of leaf area losses in tree canopies may seriously underestimate the actual herbivory, due both to the logistical problems of reaching upper foliage and to the time constraints of field research. This long-term, comprehensive study attempts to quantify inter- and intraspecific variability in herbivory of some Australian rain forest trees, and also to compare these results with other short-term studies.

## METHODS

Sites and species selection.—Research was conducted in the three major types of rain forest in New South Wales: subtropical, cool temperate, and warm temperate. Two sites of each formation were compared between the northern (Dorrigo or New England National Parks) and southern (Royal National Park) regions of the state. Site descriptions and profile diagrams are listed elsewhere (Lowman 1986a). Five species of canopy trees were measured for both leaf growth dynamics and herbivory from 1979–1988, including *Doryphora sassafras* Endl. (Monimiaceae), *Dendrocnide excelsa* (Wedd.) Chew (Urticaceae), *Nothofagus moorei* (F. Muell.) (Fagaceae), *Toona australis* (F. Muell.) (Meliaceae), and *Ceratopetalum apetalum* D. Don (Cunoniaceae).

Additional species were measured over shorter periods of time to supplement the main body of data. Species descriptions and pilot studies to determine the experimental design within the canopy of each species are listed elsewhere (Lowman 1985).

METHODS OF SAMPLING LEAVES IN TREE CANOPIES.—Branches and individual leaves along the branches were permanently marked in order to conduct quantitative observations on leaf growth dynamics. Branches were marked during February–April 1979, and observations conducted monthly for at least four years, or when leaves fell (which, in a few cases, has not occurred yet!). Leaves were numbered sequentially from the base upwards, with branches usually consisting of 8–15 leaves. Black waterproof pens were used to inscribe numbers on the adaxial surface. Branches were checked monthly for leaf emergence, senescence, tearing, desiccation, herbivory, epiphylly, or other aspects of leaf growth dynamics.

Rope climbing techniques (Perry 1978) were used to sample in the upper canopies to a height of 25 m, supplemented by ladders for trees whose trunks appeared rotten.

Two different methods for measuring herbivory of leaves were employed. "Discrete sampling" involved the random collection of at least 30 leaves from a defined region of a canopy. Old leaves (*i.e.*, > 1 yr) were collected, except in cases where specific age classes of leaves were being compared. This method, albeit quick and commonly used in the literature, assessed defoliation without respect to the seasonality of grazing or without any measure of leaves that may be totally eaten. The second method, "long-term sampling," involved monthly measurement of leaf areas on several hundred leaves of each of the five species using an area meter (Lambda model 3000) and leaf tracings. The numbers of leaves ranged from 242 to 1967 per species during the course of fieldwork (due to differences in leaf growth and senescence patterns). In cases where obvious amounts were eaten (0, 50 or >95% leaf area missing), the percentage estimates were made by eye rather than by machine.

Previous analyses of leaf phytochemistry (Lowman & Box 1983) and toughness (Feeny 1970, Lowman & Box 1983) are referred to in the interpretation of results.

PRESENTATION OF DATA.—For this study, herbivory was expressed in percentages of total leaf area missing. This method was considered preferable to expressing results in terms of real areas ($mm^2$). It facilitated comparisons between species with different leaf sizes. It was a simple matter to convert percentages into real leaf surface areas ($mm^2$) missing, since average leaf size was known; and, percentage losses remained the same throughout the expansion of a young to an old leaf (Lowman 1987) so that leaf age was not a source of error when comparing herbivory among different leaves.

Measurements were expressed as average annual percentages. Annual herbivory measurements represented the entire lifetime of damage to species whose leaves lived only one year (*e.g., T. australis*), but it represented only half the entire lifespan's herbivory to species whose leaves lived for two years (*e.g., N. moorei*). In many instances, such as *N. moorei*, the average annual herbivory (30%) was further broken down into two age-related components: approximately 60 percent herbivory to young leaves in their first year, and <1 percent damage during their second year. Average annual herbivory could be transformed into cumulative herbivory by multiplying by the number of years a leaf lived, or into daily rates by dividing by 365.

Herbivory data for sassafras were further analyzed with respect to factors of light, height, site, individuals, and leaf age. Data were transformed into log $(x + 1)$ to obtain homogeneity of variance, and multiple factor analyses of variance were performed to assess the significance of each factor. Student-Neuman-Keuls tests were used to rank the means (Snedecor & Cochrane 1967).

METHODS OF ASSESSING ANNUAL TURNOVER OF LEAF MATERIAL.—Annual proportions of leaf area lost to herbivores were compared with annual turnover of leaves to decomposers, using data obtained in litter trap studies (Lowman 1988). Estimates of both potential (*i.e.*, before insect consumption) and actual (*i.e.*, after herbivory) canopy were calculated for each rain forest formation. These data are compared and discussed in terms of the relative importance of herbivory in rain forest ecosystems and elsewhere.

## RESULTS

The variability of herbivory levels within canopies of one species (*Doryphora sassafras*) is illustrated in detail and compared to other species and sites in a more general fashion. Sassafras is the only canopy species found throughout three rain forest formations along the elevational gradient of New South Wales: cool temperate, warm temperate, and subtropical.

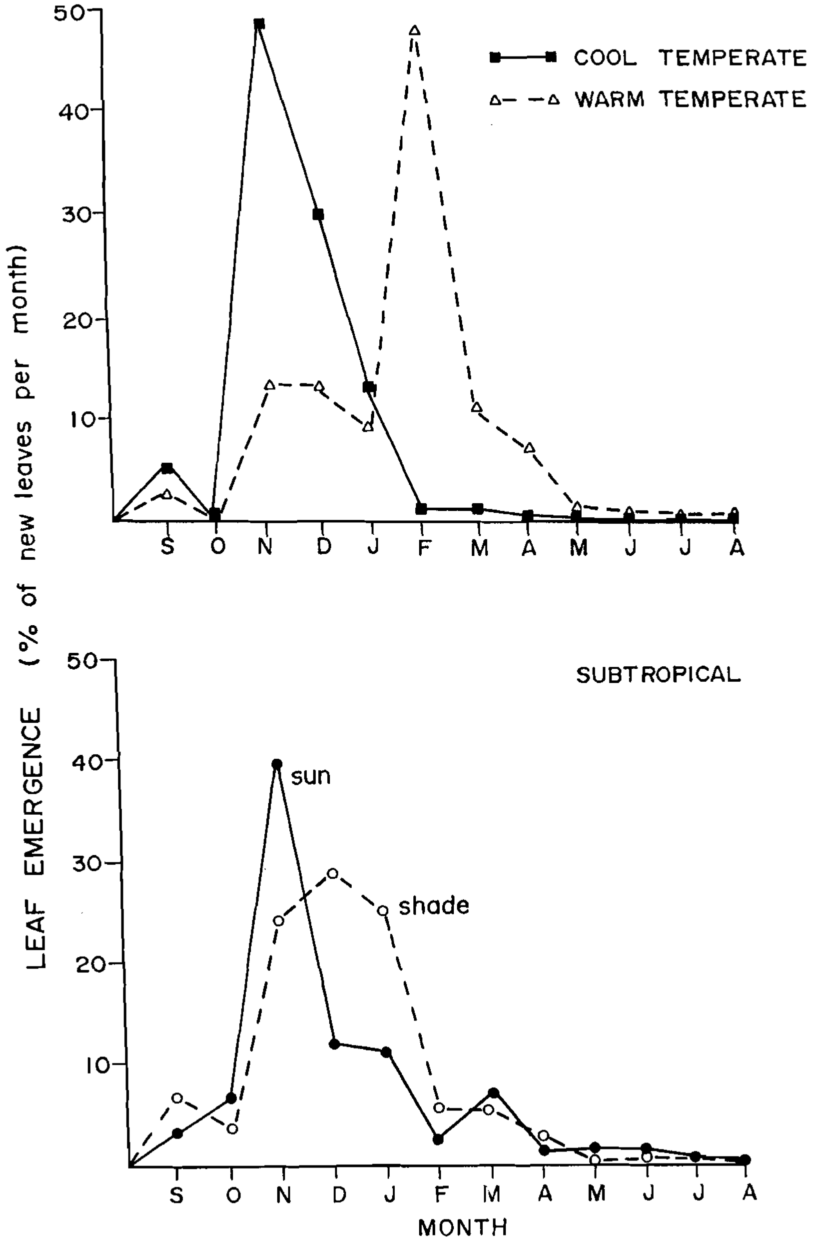


FIGURE 1. Leaf emergence for *Doryphora sassafras* in three rain forest formations of New South Wales: cool temperate, warm temperate, and subtropical (the latter including both sun and shade regions of the canopy). Data are expressed as percentage of new leaves emerging per month over one year (see text for number of leaves sampled per site).

Leaf growth dynamics of sassafras.—Both leaf emergence (Fig. 1) and herbivory (Fig. 2) peaked in summer for sassafras, fluctuating with elevation of site. Leaves emerged earlier in the cool temperate sites than at lower elevations and earlier in sun than in shade.

Leaf longevity of all leaves surviving to the mature leaf stage, *i.e.*, at least 12 months (Lowman

& Box 1983), averaged 29 months for sassafras in all sites, but varied with forest type and with light. The mean longevity for subtropical leaves was 24.5 months (but ranged from $<1$ month to $>10$ yr). In the warm temperate sites, sun leaves lived 24 mo and shade leaves 76 mo, and in the cool temperate sites, 53.8 mo (all light levels being homogeneous throughout the canopy).

Defoliation paralleled the patterns of leaf emergence since most insects preferred to eat new foliage. Herbivory was bimodal in the warm and cool temperate forests, exhibited one summer peak in the subtropical, and was negligible in all three forest types during winter months (Fig. 2). Annual leaf area losses ranged from 12.3 percent in the cool temperate sites to 30.4 percent in the low, shade leaves of the subtropical canopies (Fig. 3). Within each site, insects ate almost exclusively young leaves in both sun and shade regions of the canopy, with $<1$ percent leaf area losses incurred after a leaf's first year (Fig. 3). Herbivory was consistently higher for shade than sun leaves: 16.3 percent *vs.* 13.4 percent in the subtropical and 27.6 percent *vs.* 17.6 percent in the warm temperate.

Herbivory among four individual trees at one site (subtropical) was similar ($F_{3,76} = 0.17$, NS), as was herbivory between different sites of one forest type ($F_{2,117} = 0.55$, NS). Leaf area losses between sun and shade leaves in subtropical sites, however, were statistically different ($F_{1,58} = 5.89$, $P < 0.05$); but herbivory among leaves at different heights (with similar light levels) were similar ($F_{2,72} = 1.87$, NS).

Leaf toughness and phenolics were analyzed in relation to levels of herbivory (Fig. 4). Leaves increased dramatically in toughness as they matured, with a high correlation between toughness and herbivory ($r^2 = 0.90$). Leaves were tougher in the sun (*vs.* shade) and in sites at higher elevations. Phenolics (measured as total phenols and condensed tannins) were less highly correlated with herbivory ($r^2 = 0.55$), although sassafras had the highest levels of phenolics measured among five rain forest species (Lowman & Box 1983).

Leaf fall was a summer event for sassafras, occurring simultaneously with leaf emergence; although the trees were always evergreen because most leaves lived $>2$ yr (Fig. 5). Leaf decay was slowest in the cool temperate formation, requiring $>3$ yr for half the leaves to disappear (Fig. 5). Leaves on the subtropical forest floor decayed 4 times more quickly, disappearing in only 1.5 yr.

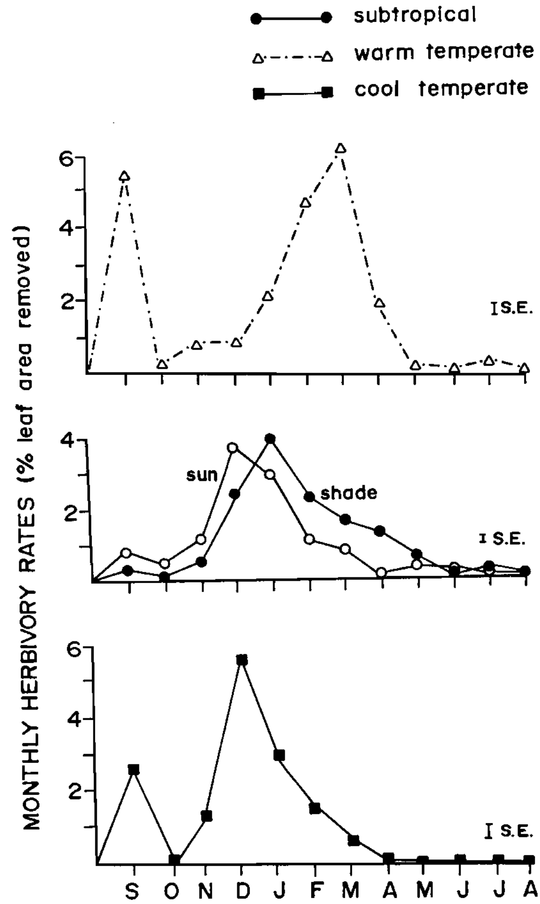


FIGURE 2. Herbivory of *Doryphora sassafras* in three rain forest formations of New South Wales: cool temperate, warm temperate, and subtropical (with sun and shade regions of the canopy included in the warm temperate graph). Data are expressed as percentage of leaf area removed per month, averaged over a four year duration (see text for number of leaves sampled per site).

VARIABILITY IN HERBIVORY AMONG CANOPY SPECIES.—Annual herbivory was as low as 3.3 percent in *T. australis* and as high as 48.4 percent for *A. trifoliatum* (Fig. 6). For almost all species, young leaves were preferred by insect herbivores, as were shade leaves. Leaf toughness was highly correlated to defoliation levels in most species (Lowman & Box 1983).

The range of variability among species was even greater when compounded with the factors of site and individual trees (Fig. 6). For example, three site averages for *N. moorei* ranged from as low as 22.5 percent to as high as 43.5 percent, with individual trees up to 67.5 percent (Selman & Lowman 1983). *T. australis,* albeit with lower herbivory than any other species, had an average of 3.3

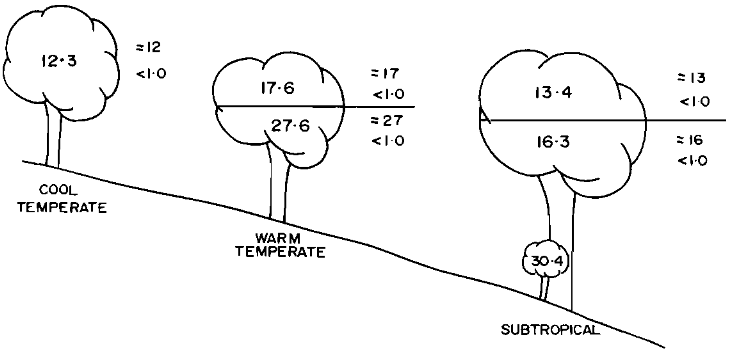


FIGURE 3. Average annual herbivory levels (expressed as percentage leaf area loss) for *Doryphora sassafras* along an elevational gradient in New South Wales, including cool and warm temperate, and subtropical rain forests. The lower two sites had significantly different herbivory in sun (upper canopy) and shade (lower canopy) leaves. Numbers to the right of each tree and canopy section indicate percentage leaf area losses for new leaves (upper number of each pair) and old leaves (lower number of each pair).

percent at one site and twice that amount (6.3%) at a more northerly site.

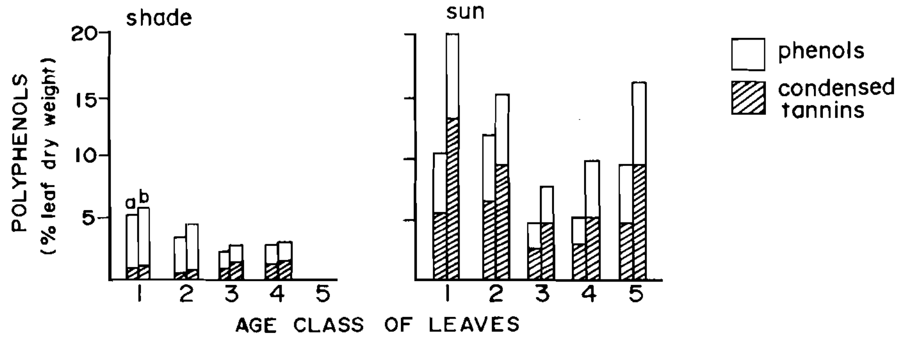
VARIABILITY IN HERBIVORY BETWEEN TWO SAMPLING METHODS.—Many researchers have utilized discrete sampling whereby leaves are harvested and measured for holes missing (*e.g.*, Odum & Ruiz-Reyes 1970, Fox & Morrow 1983, Proctor *et al.* 1983). In contrast, long-term measurements involve the permanent marking of leaves throughout a tree canopy and repeated measurements of increments defoliated throughout the life of a leaf. Long-term sampling provided a more comprehensive estimate of herbivory, since leaves that were totally eaten could be accounted for as well as leaves only partially eaten. There was a two- to fourfold discrepancy between estimates obtained by these two methods (Table 1). The potential error ranged from almost negligible in sassafras leaves in the cool temperate sites (where no young leaves were totally eaten), to a discrepancy of 3.9 for sun leaves in the warm temperate sites (where almost one of every four leaves were totally eaten and therefore not accounted for by discrete sampling). Overall, long-term measurements resulted in estimated losses 2.8 times higher than the discrete sampling method.

ANNUAL TURNOVER OF LEAF MATERIAL IN AUSTRALIAN RAIN FORESTS.—In this study, between 14 percent and 27 percent of the total canopy was consumed by herbivores annually (Fig. 6). This loss is relatively high, especially when compared to the annual turnover of leaf material to decay (Table 2). In these evergreen forests, approximately one-half of the actual canopy fell annually to decomposers (*i.e.*, 39%), yet the average annual defoliation was 21 percent,

TABLE 1. *Differences between two sampling methods for measuring herbivory of* Doryphora sassafras *(N = 200 leaves).*

| Site | Commonness[a] | Long-term |  | Discrete |  | Discrepancy (L/D) |
|---|---|---|---|---|---|---|
|  |  | Mean | (SEM) | Mean | (SEM) |  |
| Cool temperate | 14 | 12.3 | (1.8) | 12.0 | (1.2) | 1.0 |
| Warm temperate | 20 |  |  |  |  |  |
| sun leaves |  | 17.6 | (2.2) | 4.5 | (0.9) | 3.9 |
| shade leaves |  | 27.8 | (2.6) | 7.6 | (0.9) | 3.7 |
| Subtropical | 10 |  |  |  |  |  |
| sun leaves |  | 13.4 | (2.0) | 4.4 | (0.7) | 3.0 |
| shade leaves |  | 16.3 | (2.2) | 6.4 | (0.7) | 2.5 |
| Mean |  |  |  |  |  | 2.8 |

[a] Percent forest canopy biomass comprised of *D. sassafras*.



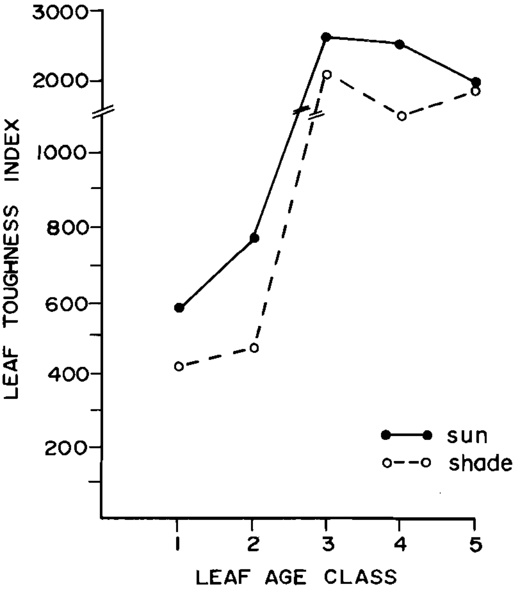


FIGURE 4. Phenolics and leaf toughness as indicators of leaf palatability of *Doryphora sassafras* in subtropical rain forests of New South Wales. Polyphenols are expressed as percentage leaf dry weights of both phenols and condensed tannins for two trees (labeled a and b), whose leaves were ranked from young (age class 1) to old (age class 5). Methods and age class definitions are listed elsewhere (Lowman & Box 1983). Leaf toughness represents the average penetrometer pressure required to puncture five holes in each of three leaves per sample point, using methods of Feeny (1970).

nearly half that (Table 2). In forests where leaf longevity is greater than one year and the annual herbivory is retained to the next season, defoliation levels are cumulative and affect the energetics of the canopy longer than in their deciduous counterparts in northern temperate forests.

In northern deciduous forests, the ratio of leaf turnover by decay to leaf turnover by herbivory is

TABLE 2. *Annual turnover of* D. sassafras *leaf material in Australian rain forests* $(t \cdot ha^{-1}\ yr^{-1})$.

| | Leaf fall | | Herbivory | | | |
|---|---|---|---|---|---|---|
| | Amount | % of total canopy | Amount | % of total canopy | Actual canopy | Potential canopy |
| Cool temperate | | | | | | |
| sassafras only | 0.51 | 44% | 0.14 | 12.3% | 1.02 | 1.16 |
| total forest | 3.53 | 36.5% | 2.63 | 27% | 7.06 | 9.69 |
| Warm temperate | | | | | | |
| sassafras only | 0.25 | 35% | 0.16 | 22.7% | 0.55 | 0.71 |
| total forest | 4.05 | 35% | 2.5 | 22% | 8.91 | 11.41 |
| Subtropical | | | | | | |
| sassafras only | 0.56 | 42% | 0.2 | 15% | 1.12 | 1.32 |
| total forest | 5.59 | 46% | 1.76 | 14% | 10.5 | 12.26 |

approximately 10:1 (reviewed in Bray & Gorham 1964). In the Australian rain forests, the ratio averaged almost 2:1, with 39 percent falling to the forest floor and 21 percent consumed by insects annually (Table 2). In sassafras alone, the ratio was just under 3:1 with 41 percent decay and 16 percent herbivory.

## DISCUSSION

Three possible sources of error must be considered when comparing the results of different herbivory

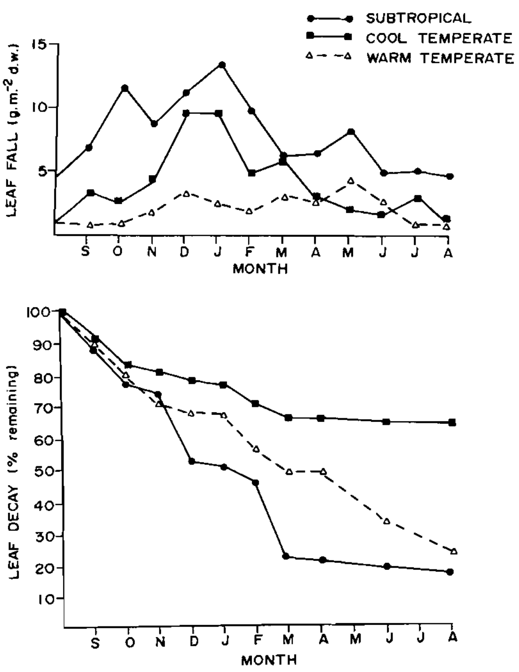


FIGURE 5. Leaf fall and leaf decay for *Doryphora sassafras* in cool temperate, warm temperate, and subtropical rain forests of New South Wales. Leaf fall is expressed as g/m$^2$ d.w./mo, averaged from three litter traps per site over two years. Leaf decay is expressed as percentage d.w. remaining (in mesh bags of leaves left on the forest floor, 30 g original fresh weight), averaging 3 bags per month at each site. Details of methods are described elsewhere (Lowman 1988).

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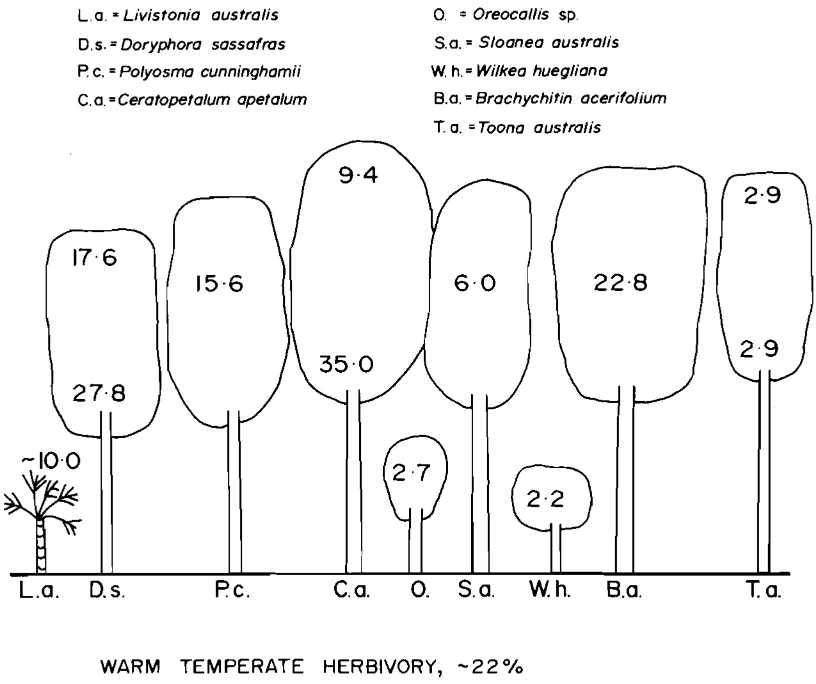
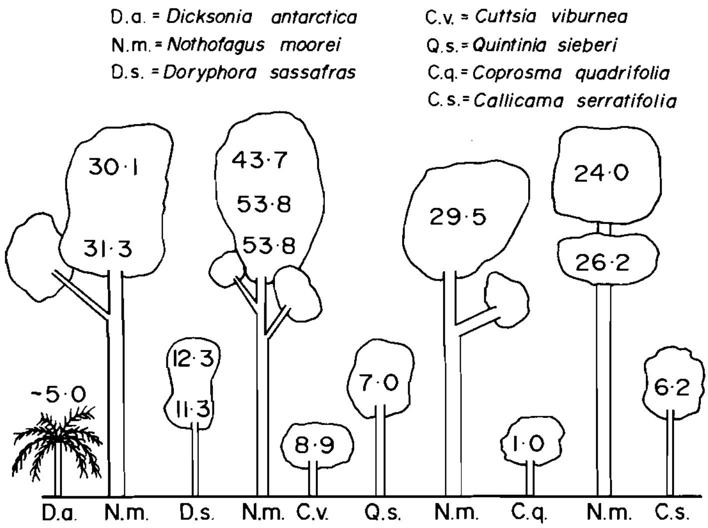
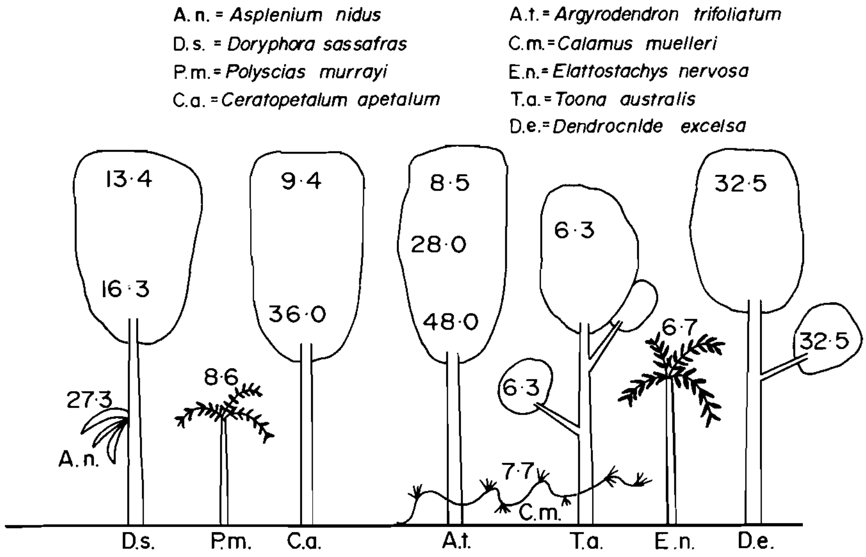


FIGURE 6. Herbivory levels in cool temperate, warm temperate, and subtropical rain forests of New South Wales. Data are expressed as percentage leaf area loss per year for each species, in some cases patchy among different regions of its canopy.



COOL TEMPERATE HERBIVORY, ~27%



SUBTROPICAL HERBIVORY, ~14·6%

studies. Different sampling methods may produce results that vary by as much as fourfold (Table 1). Discrete sampling, albeit quick and widely used, can underestimate the true amount of leaf area losses in canopies, if some leaves are entirely eaten. For species whose leaves are never entirely eaten (*e.g.*, *T. australis*), discrete sampling is an efficient, accurate method. But for species whose leaves are often entirely eaten (*e.g.*, *D. sassafras*), discrete samples can underestimate primary consumption by two- to fourfold (Table 1).

Herbivory is patchy throughout different regions of the canopy, and sampling that is restricted to the lower canopy, to one site, or to only one light regime will invariably produce a biased result. In Australian rain forests, herbivores showed feeding preferences with respect to at least five factors: age of leaf tissue, species, light, height, and site. Leaf sampling must include replicates of all these variables to accurately measure defoliation. Other factors may also be important, such as the successional status of tree (Coley 1982).

An adequate sampling regime requires information on insect feeding biology, rather than just leaf area losses. Leaf palatability (Lowman & Box 1983) and numbers of herbivores in a forest have obvious effects on grazing levels; even trophic levels of insects may vary among forests, as has been speculated in eucalypts (Fox & Morrow 1985). It remains difficult, however, to distinguish between relative differences in insect populations among forests until field methods have been better standardized (Lowman 1986b), because the variability in methodology is immense.

The removal of leaf tissue by primary consumers at proportions of up to approximately 30 percent of canopy area in some Australian rain forests is surprisingly high compared to that of other studies (*e.g.*, Leigh & Windsor 1978, Wint 1983, Odum & Ruiz-Reyes 1970, Benedict 1976, Wiegert 1970), where levels of 3–10 percent have been estimated. The remaining 90–97 percent is considered to have been incorporated into the decay pathway as fallen leaves, and so the grazing pathway appears relatively small in contrast (Hairston *et al.* 1960). However, in an evergreen rain forest tree where the leaves live >1 yr, insect damage incurred to young leaves remains incorporated in the canopy region for at least twice the duration of deciduous leaves. An accurate calculation of leaf material turnover ro both herbivory and decay requires more than simply measuring discrete amounts of holes in leaves. It requires information on leaf longevity and on amounts of defoliation to different leaf cohorts throughout the canopy. Furthermore, if young leaves are occasionally eaten entirely, these 100 percent losses must also be measured.

## CONCLUSIONS

The resource of green foliage in a rain forest is not a homogeneous array of food; nor is it a random array of tattered and hole-riddled leaves. There are factors regulating herbivory, and patterns are emerging: levels of defoliation are higher in young than in old leaves, in shade than in sun leaves, in lower than in upper canopy leaves, in certain species than in others. I have quantified aspects of herbivory in Australian rain forest canopies, with particular emphasis on the resource availability of sassafras on a micro- (or within-canopy) scale. But this is still only half the picture. We need to know more about the population biology of the herbivores, and also to know about the variability in resources among sites and soils and trees that ultimately lead to patchiness in levels of herbivory measured.

## ACKNOWLEDGMENTS

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