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Temporal and spatial variability in insect grazing of the canopies of five Australian rainforest tree species

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Abstract

Herbivory was measured monthly for 2 years on leaves of permanently marked replicate branches in the canopies of five Australian rainforest tree species. Variability in insect grazing activities was evident with respect to several factors:

1. leaf age — young leaves were preferred over older leaf tissue;

2. height — leaves closer to ground level were more heavily grazed;

3. light — shade leaves were preferred to sun leaves;

4. time — grazing was intense during spring and summer months, and almost negligible during autumn and winter, but was cumulatively similar between the 2 years;

5. space — grazing was extremely variable on small spatial scales such as between individual leaves and branches, but similar where hundreds of leaves were pooled on larger scales between individual canopies and among geographically different sites;

6. tree abundance — grazing was heavier at sites where a tree species was common than where it was rare;

7. host tree species.

Long term observations resulted in higher but more accurate estimates of herbivory since it was possible to quantify losses of leaves totally eaten, an event not accounted for in field methods of discrete sampling whereby leaves are merely harvested and measured for area missing. Variability in herbivory is discussed in terms of plant–insect phenologies, plant defences, successional status of tree species, and insect behaviour.

Introduction

The impact of insect herbivores on forest communities ranges from moderate levels of defoliation as in northern temperate forests (e.g. Bray 1961, 1964; Reichle *et al.* 1973; Nielson 1978) and some tropical rainforests (Odum & Ruiz-Reyes 1970; Leigh & Smythe 1978), to more extensive damage as in some Australian eucalypts (Carne 1966; Journet 1981; Lowman, unpubl.) and many forest plantations (Ohmart 1984). Defoliation levels in natural, undisturbed forests usually range from 3–10% leaf area losses, according to most reports in the literature, although most figures are based upon studies of short duration and scope (when one considers the seasonal fluctuations of insect populations and the vast number of leaves in a forest).

The literature on plant-insect relationships has expanded greatly during the past few years, and it has become apparent that these interactions are extremely complex. Grazing of leaves by insects can be extremely variable, depending upon factors such as light regime (Maiorana 1981), successional status of tree (Coley 1982), species (Fox & Morrow 1983), site (Morrow & Fox 1981), nutrient levels of substrate (Onuf *et al.* 1977), age of leaf tissue (Wint 1983) and others. With this increased awareness of the complexity of plant-insect relations, the methods of sampling must become more extensive in order to account for variability. For example, recent work by Coley (1982) in neotropical forests involved the measurement of several thousand leaves over several months, and she showed that herbivory is higher than previously assumed, with 21% (and higher in pioneer species) leaf area losses on saplings of canopy trees. Unfortunately, rainforest canopies are difficult to sample, due to the complexity of both species composition and structural features. There are many species, canopy heights, light regimes, types of vegetation, and age classes of leaves, all with potentially different susceptibility to grazing. Also there are logistical problems associated with access to the upper levels of canopy, where most of the leaves occur. An accurate assessment of rainforest herbivory requires long term sampling throughout a range of canopy regions and species, including both upper and lower branches.

The objectives of this study were twofold: to accurately quantify grazing by insects in Australian rainforests, and to examine temporal and spatial variability in herbivory throughout different regions of the canopy. In addition, the accuracy of different methods of sampling are discussed, and compared to studies reported in the literature. Additional aspects of leaf growth dynamics in rainforest canopies — including leaf emergence, turnover of leaf material to decomposers, factors of leaf mortality other than insects, and leaf longevity — have been recorded elsewhere (Lowman 1982b).

Methods

Descriptions of sites and species

Research was conducted in the three major types of rainforest in New South Wales, Australia (Fig. 1). Two sites of each formation were compared between geographically different parts of the state where possible:

1. Subtropical rainforest in Dorrigo National Park (30° 20'S, 800 m), in north-central NSW, defined by Webb (1959) as complex notophyll vine forest (CNVF), and in Mt Keira Preserve near Wollongong in south-central NSW (34° 30'S, 400 m).
2. Warm temperate rainforests in Dorrigo National Park, Never Never Region in north-central NSW (30°, 20'S, 800 m), and Royal National Park (34° 10'S, 20 m) in south-central NSW, simple notophyll vine forest (SNVF) (Webb 1959).
3. Cool temperate rainforest in three sites of the New England National Park in north-central NSW (30° 30'S, 1200 m), mossy microphyll fern forest (MMFF) (Webb 1959).

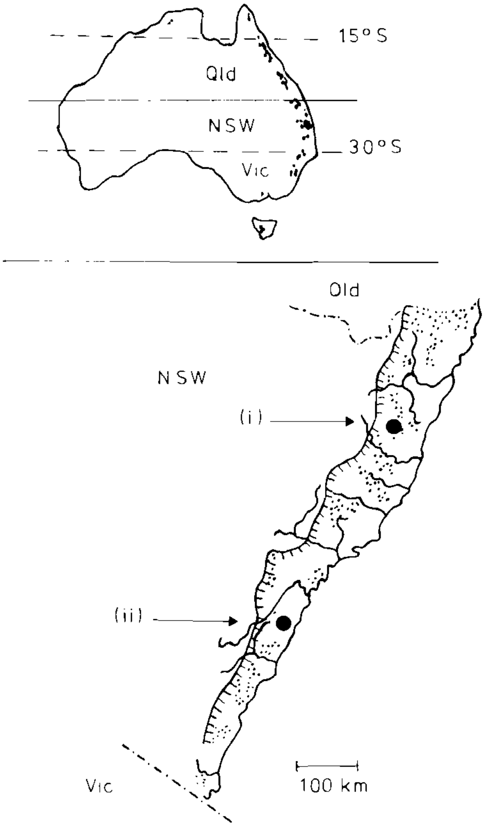

FIG. 1. (a): Location of Australian rainforests, distributed discontinuously down the east coast. (b): New South Wales coastline, depicting western boundary of rainforest distribution and study sites. (●): (i) New England and Dorrigo National Parks. (ii) Royal National Park and Mt Keira Reserve.

Five canopy tree species (Table 1) were chosen for field measurement and observation, each selected for representativeness of one of the three rainforest types in NSW, and for having leaf morphological characteristics of particular relevance to plant–insect interactions (e.g. presence of hairs or heavy cuticle, or variability in growth patterns including deciduousness and evergreen).

Determination of leaf 'populations' in rainforest canopies

Preliminary leaf samples were collected to examine the variability of morphological characteristics of the leaves (e.g. shade and sun leaves) within and among species as an index of potential susceptibility to grazing. These pilot studies identified different types of leaves (termed leaf 'populations') within the canopies of each species, thereby enabling the establishment of a balanced programme of field sampling to include leaves from all distinct regions of canopy. Observations were conducted during one growing season (October-March 1978–79) prior to commencement of this study, to gain familiarity with leaf growth habits, morphological characteristics, and age classes. During February-April 1979, samples of 30 mature leaves were harvested from different sections of the canopies of all five species with respect to environmental factors: light regime (sun versus shade), height (0–3 m, 3–7 m; > 7 m), site, aspect (N, S, E, W), and individuals (at least three trees of each species at each site). Samples from the upper canopy (20–30 m) were collected with a slingshot or shotgun. The length and area of leaves were measured, these two variables representing morphological characteristics that may reflect differences in leaves throughout the canopy. Multiple factor analyses of variance were performed on the data [which were transformed to log (x) to obtain homogeneity of variance] to determine significantly different leaf 'populations' throughout the canopy. The experimental design for sampling defoliation on each species was based upon this initial assessment of the variability of the morphology of the leaves.

Leaf age classes were also defined during extensive months of phenological observations prior to field monitoring, as follows (see also Lowman & Box 1983):

1. young leaf — usually 0–2 weeks old, after budburst but before leaf is full-sized;
2. youthful leaf — usually 2–4 weeks old, leaf that is full-sized but still lacking in attributes that comprise a mature leaf such as heavy cuticle or deep green pigmentation;
3. mature leaf — approximately 1 month after emergence until the end of its first year; fully grown and structurally developed;
4. old leaf — mature leaves in their second year, distinguished from previous class by position on the branch, by darkening (shade leaf) or yellowing (sun leaf), and often by first signs of epiphylly or senescence;
5. senescent leaf — leaf in the process of dying and soon to fall; distinguished by basal position in branch hierarchy, loss of chlorophyll, or onset of decomposition.

Long term monitoring of canopy leaves

Branches and individual leaves along the branches were permanently marked in order to conduct quantitative observations on leaf growth dynamics. A leaf-monitoring station consisted of at least three branches, located in all regions of canopy where the leaves were morphologically different as determined by preliminary measurements (Table 2). For example *C. apetalum* required different leaf-monitoring stations among sites, light, regimes, heights (but not aspect), since these variables showed statistical differences between populations of leaves. Since all canopy samples were defined according to these variables, it was also possible to examine leaf growth with respect to each individual factor as well as generally by species and site. The numbers of leaves, branches, and trees sampled are listed in Appendix 1.

Branches were marked initially during February-April 1979, well before the spring flush for that year (September-October), and observations were conducted monthly for at least 2 years. Leaves were numbered sequentially from the base upwards, with branches usually consisting of 8–15 leaves. Black waterproof Pentel pens were used to inscribe numbers on the adaxial leaf surface. The ink usually lasted up to 1 year before fading, in which case the numbers were remarked. The ink did not result in mortality or deformation of the leaves, and herbivores occasionally ate through the ink, obviously undeterred by its presence. Subsequent new leaves were marked as they emerged, and lateral new leaves were indicated by a hyphenated number (e.g. budburst from the base of a leaf originally numbered as 3 would result in a sequence of new leaves numbered, 3-1, 3-2, 3-3 etc.). Monthly observations were recorded, and branches were checked for leaf emergence, senescence, tearing, desiccation, epiphylly, or any other aspect of leaf growth dynamics.

In some cases, it was necessary to establish leaf-monitoring stations in the upper canopy. Two methods were employed that enabled establishment of permanently marked sites in the upper canopy similar to the leaf-monitoring stations in the lower canopy. In the cool temperate rainforest where beech wood is often soft and rotten, ladders constructed of hard *Eucalyptus* timber were tied against tree trunks with nylon webbing.

Rope-climbing techniques (Perry 1978; Landsberg & Gillieson 1982) were used to sample in the canopies of *D. sassafras, C. apetalum, T. australis,* and *D. excelsa*. Access to the canopy of the last was facilitated by climbing an adjacent tree (since this species has weak wood and hazardous stinging hairs on leaves and stems). Where there was significant leaf variation with height or light, vertical transects were established through the canopies of at least three individuals of each species per site. Climbing techniques expanded the range of leaf sampling from ground level to approximately 20 m in height, thereby including all the leaf populations within the canopies as defined in Table 2. Further details on site characteristics (species diversity, structure of stands, canopy height, etc.) are listed elsewhere (Lowman 1982b).

Herbivory measurements

Long term observations. Changes in the amount of leaf area missing per leaf were measured monthly

TABLE 1. Leaf and growth associated characteristics of five Australian rainforest trees

Species and family	Habitat	Phenology and growth	Leaf features	Tree architecture (Halle *et al.* 1978)	Reference
Ceratopetalum apetalum D. Don (coachwood) -Cunoniaceae	warm temperate	evergreen, manifold, late successional	lanceolate, fine-toothed, hard cuticle, pulvini, simple, opposite	Rauh	Edinb. New. Phil. Jour. IX, 94, 1830; Francis 1970
Doryphora sassafras Endl. (sassafras) -Monimiaceae	warm and cool temperate, subtropical	evergreen, manifold, late successional	elliptical, aromatic, hard and waxy cuticle, opposite, coarse-toothed, simple	Rauh	Incongr. t.10, 1838; Francis 1970; Floyd 1978
Dendrocnide excelsa (Wedd.) (giant stinging tree) -Urticaceae	subtropical, disturbed sites	evergreen, continuous, early successional (invader)	cordate, succulent, stinging hairs, toothed, alternate simple	Aubreville	Chew 1969; Francis 1970; Maiden 1928; Floyd 1977
Nothofagus moorei F. muell (beech) -Fagaceae	cool temperate	evergreen, intermittent, climax	elliptical, fine-toothed, brittle, simple, alternate	Troll	Ann. Nat. Hofmas; Wien XI, 1886; Francis 1970; Floyd 1977.
Toona australis F. muell (red cedar) -Meliaceae	subtropical	deciduous, intermittent, late successional	ovate-lanceolate, entire, alternate, often downy, thin cuticle, compound	?	Nat. Pflanzen-familien III, 4, 27c 1896; Francis 1970; Floyd 1979.

TABLE 2. Results of analyses of variance of leaf length and leaf area — determination of leaf 'populations' within and among rainforest canopies

Species	Light	Height	Aspect	Among individuals	Among sites
N. moorei	† sun < shade	† 10 = 5 < 1 m	n.s.	n.s.	n.s.
D. sassafras	‡ sun < shade	‡ 20 < 10 = 1 m	n.s.	n.s (RNP: *)	* NEP < DNP = Mt K < RNP
C. apetalum	‡ sun < shade	† 20 < 10 < 1 m	n.s.	n.s.	* DNP = Mt K < RNP
D. excelsa	n.s.	n.s.	n.s.	n.s.	n.s.
T. australis	n.s.	n.s.	n.s.	n.s.	n.s.

* indicates $P < 0.05$, † indicates $P < 0.01$, ‡ indicates $P < 0.001$. RNP Royal National Park, DNP Dorrigo National Park, NEP New England National Park, Mt K Mt Keira Boy Scout Reserve.

on several hundred leaves for each of the five species using an area meter (Lambda model 3000) and leaf tracings. The numbers of leaves varied from 242 – 1967 per species per month due to differences in leaf growth and senescence patterns (Appendix 1). The number of branches monitored per species varied depending upon the different leaf populations that required sampling (Table 2). The areas of leaves which had been removed by grazing were traced and measured with the area meter. In cases where obvious amounts were eaten (0, 25, 50, or greater than 75% leaf area lost), the percentage estimates were made by eye rather than by machine. Amounts grazed were recorded monthly for 3 years (and more frequently when possible), and cumulatively for the duration of the life of a leaf.

For each leaf, the mean monthly increment eaten by herbivores was expressed as a proportion of the total intact (or potential) leaf area (PLA), calculated by:

$$1.00 - \frac{\text{ALA}}{\text{PLA}} - \begin{array}{l}\text{amounts grazed}\\ \text{in previous}\\ \text{months}\end{array} = \begin{array}{l}\text{proportion grazed}\\ \text{in current month}\end{array}$$

The annual herbivory rate simply represented a cumulative proportion eaten during 12 months (e.g. a beech leaf may have lost 5% leaf area in September, an additional 10% in October, and 0% during the remaining 10 months, giving an annual grazing loss of 15%).

Mortality due to grazing was distinguished from natural senescence based upon the time of year, speed of disappearance, and leaf age. The disappearance of a young leaf, where grazed portions steadily increased toward 100% during months when herbivores were active, was tallied as 'totally eaten'. A mature leaf that had not been grazed during the past year and then was suddenly absent at a monthly observation was tallied as 'senesced'. Similarly, a young leaf that disappeared entirely with no evidence of grazing (e.g. frass) was also tallied as 'leaf fall', assumed due to abrasion or wind.

It is conceivable that some events recorded as leaf fall were due to herbivores which feed extremely rapidly and patchily (e.g. stem borers). Such feeding would not be obvious in monthly records of incremental changes in leaf area. Herbivory rates calculated from long term observations, therefore, were reflections of only directly observed grazing activities, and may be slight underestimates since some leaves assumed to have fallen may have been eaten instead.

Herbivory data were expressed by proportion (% missing) rather than actual increments (cm^2) eaten. This approach was used for three reasons:

1. Herbivores often chewed holes in young leaves and data expressed as actual area missing from an adult leaf may be misleading, since the areas consumed from the young leaf would expand as the leaf matured; but the proportion removed would remain approximately the same (Reichle *et al.* 1973).

2. Since leaf size was extremely variable both between and within species, a percentage loss is more useful in comparing rates of herbivory among species and extrapolating in terms of loss from an entire canopy (e.g. 2 cm^2 missing from a 15 cm^2 red cedar leaflet is a much greater proportional loss than 2 cm^2 from a 200 cm^2 stinger leaf).

3. Most studies in the literature estimate herbivory as percentage lost; conforming to this thereby facilitates comparisons with other studies.

In some cases, it may be useful to calculate loss of leaf area in terms of actual area missing rather than by proportions alone (particularly for estimating insect populations as reflected by holes in leaves in cases where an insect's damage is specifically recognized), or for determining amounts of food available for herbivores. The actual area eaten from young leaves was estimated from holes in fully expanded leaves using regression equations (Lowman 1982b). In addition, mean leaf areas were calculated, allowing transformation of the percentage missing data to actual leaf area eaten (Lowman 1982b).

Herbivory data for leaves were pooled by species to obtain canopy means and some species further sub-analyzed with respect to the factors of light, height, site, individuals and leaf age. Data were transformed to log (x + 1) to obtain homogeneity of variance and multiple factor analyses of variance were performed to determine the significance of each factor. Student Neuman-Keuls tests were used to rank the means.

Phenology of leaf emergence, leaf fall and other growth-reflected activities were recorded from the marked branches, so that grazing patterns could be related to seasonality of growth. Although the quantified information on leaf growth patterns are reported elsewhere (Lowman 1982b), the results are summarized here in conjuncton with abundance of herbivores. Since most rainforest leaves lived longer than 2 years, the monitoring was continued beyond the duration of this report.

Discrete measurements. A second method of measurement was conducted, whereby random samples of 30 leaves were collected from the canopy at different sites and times with respect to height, light, and species. Old leaves (i.e. > 1 year) were always collected, except in cases where specific age classes of leaves were being compared. This method, termed discrete sampling, assessed defoliation without direct consideration of seasonality of grazing or without any measure of leaves totally eaten. It is a much quicker method, and commonly used by many researchers to estimate herbivory. These measurements were compared with long term measurements to assess the accuracy of discrete sampling.

Herbivory losses

The results of monthly herbivory monitoring were assessed for both temporal and spatial variability within and among the five tree species. First, three temporal aspects of grazing were assessed: grazing levels among different age classes of leaves; monthly variability in herbivory throughout the canopy; and annual differences in cumulative herbivory losses. Second, spatial analyses of herbivory included the assessment of variation with respect to four spatial scales: individual leaves, branches, individual trees, and sites; and with respect to two environmental factors within the canopies (light regime and canopy height).

Results

Determination of leaf populations

The results of initial sampling to determine leaf 'populations' show that some (but not all) rainforest trees exhibit significant morphological differences as influenced by environmental factors (Table 2). Both *T. australis* and *D. excelsa* have rather homogeneous canopies in that neither leaf length nor area were significantly different with respect to any of the five environmental factors. The sampling programme for these canopies, therefore, was not designed to include extensive subsampling within different canopy sections. The other three species exhibited significant differences with respect to one or more environmental factors, and so required slightly more complex sampling programmes to adequately monitor leaf growth dynamics. *N. moorei* exhibited variability with respect to light and height, thus necessitating the establishment of sampling sites along vertical transects through the canopy and within both sun and shade regions. *C. apetalum* and *D. sassafras* exhibited significant differences with light, height, and among sites. These species required the most extensive sampling in order to provide adequate replication and coverage of canopy regions. Subsequently, the numbers of leaves, branches and trees sampled reflected this predetermined variability within canopies (tallies of samples are listed in Appendix 1).

Herbivory losses

Temporal variability of grazing:

1. Differences in herbivory with leaf age. Since every leaf was marked as it emerged on the sample branches, it was possible to quantify monthly grazing losses according to different leaf age classes (Fig. 2). Cumulative annual grazing of a canopy leaf averaged from 4.8% (*T. australis*) to 32.5% (*D.

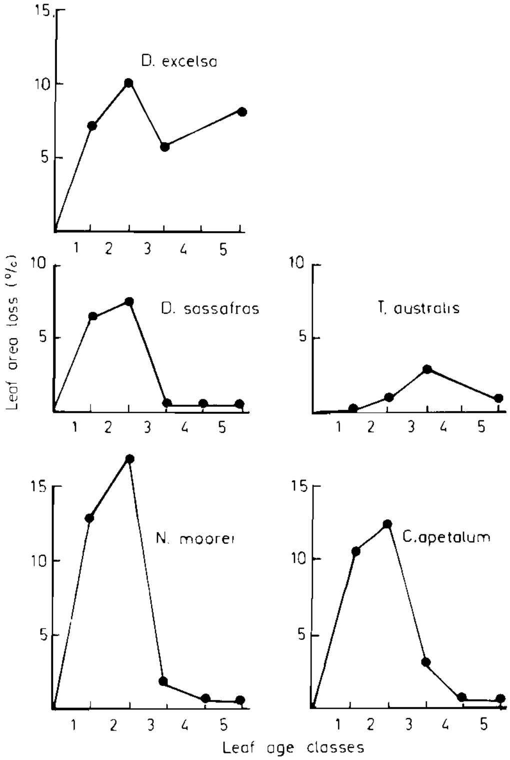

FIG. 2. Leaf area loss to insect herbivores for five different age classes of leaf tissue, in five rainforest tree species, expressed as annual percentage leaf area defoliated per leaf. See text for age class definitions.

excelsa), with intermediates of 14.5% (*D. sassafras*), 26.1% (*C. apetalum*) and 30.7% (*N. moorei*) of leaf area missing, but the leaves of each species were grazed at different intensities at different age levels. Young leaves (age classes 1 and 2) were most heavily grazed in the evergreen trees (*D. sassafras, N. moorei*, and *C. apetalum*) presumably since they were more palatable than the mature leaves characterized by tough, waxy surfaces and higher phenolic contents (Lowman & Box 1983). In *T. australis*, a deciduous species, the grazing of young as well as old leaves was negligible. In contrast, *D. excelsa* (also short-lived leaves but with evergreen canopies) had consistently high herbivory throughout the lifespan of a leaf.

The analyses of grazing in different age classes of leaves were useful for comparing different types of leaves, as morphological characteristics of the leaf were the basis for the age classes. The age classes were not equivalent in timespan (i.e. length of time vulnerable to grazing), since three species were evergreen with leaves living about 2 years, and two species had shorter-lived (less than 1 year) leaves. An analysis between two equivalent timespans was made on *N. moorei* whereby grazing of first year leaves (age classes 1, 2, 3) was compared to that of second year leaves (classes 4, 5, Table 3). Grazing was very high during year one (54% leaf area loss) but negligible during year two (0.2%). Thus, herbivores not only grazed heavily on age classes 1 and 2, but avoided leaves almost completely during their second year in the canopy.

TABLE 3. Annual herbivory rates for *N. moorei* leaves of different ages

Site	First year	Second year	Young:old ratio	$\bar{x}$ (weighted by ratio)
1	57.0	0.2	2 : 3	22.9
2	61.6	0.3	3 : 2	37.1
3	43.9	0.2	3 : 1	33.0
$\bar{x}$	54.2	0.2	4 : 3	31.0

Data based on long term observations of leaves, both partially and completely eaten. (means include three branches on three trees per site, and data are expressed as % loss of total leaf area per leaf).

Grazing damage to young versus old leaves was significantly different ($F_{1,98} = 1384.34$, $P < 0.001$), data transformed to log (x + 1) for homogeneity of variance.

2. *Monthly variability in herbivory.* When grazing of all the leaves within the canopies were averaged on a monthly basis, the seasonal patterns showed simultaneous peaks in both leaf flushing and grazing activity (Fig. 3). *D. excelsa* exhibited a continuous pattern of leaf flush and herbivores grazed throughout the year. In contrast, *N. moorei* leaves flushed synchronously during early spring (September-October) and grazing intensities peaked soon after leaf emergence, in October-November. *C. apetalum* had a major spring leaf flush with a corresponding peak in grazing levels, and a lesser late summer (March) leaf flush with an associated defoliation.

Monthly herbivory intensity varied considerably among species, with *D. excelsa* losing approximately 5% leaf area per month. Conversely, *T. australis* leaves were defoliated approximately 0.5% per month, only one tenth the amount. Subsequent studies on the leaf chemistry of these species supported these grazing differences in field observations (Lowman & Box 1983).

3. *Annual variability in herbivory.* Grazing intensity of canopy leaves differed slightly between the 2 years of field monitoring: 1979–80 and

1980–81, but was not statistically significant except in *T. australis*. Grazing was lower during the second year in all species except *N. moorei* which suffered a particularly heavy beetle infestation during 1980–81 (Selman & Lowman 1983). *T. australis*, the only species to exhibit statistically significant year-to-year variation in grazing, had relatively low herbivory during both years as compared to other species. The fact that 1980–81 was somewhat drier than the previous year (Lowman 1982b) may have led to the decline in numbers of the relatively few herbivores that grazed *T. australis* (Appendix 2). Environmental conditions (e.g. drought, cold spells) could also affect leaf chemistry and other aspects of leaf growth as well as insect abundance. Measurement of herbivory over several years' duration increases the reliability of the quantitative estimates of leaf area losses to grazers.

Spatial aspects of herbivory:

1. Light. Three species (*D. sassafras*, *N. moorei*, and *C. apetalum*) exhibited morphological differences in leaf size with light regime (Table 2) and were thus monitored extensively for herbivory in both sun and shade conditions. Shade leaves had significantly higher grazing levels than those in the sun for both *D. sassafras* and *C. apetalum* (Table 4) but not for *N. moorei*. Sun leaves of *D. sassafras* and *C. apetalum* were extremely small and tough, with higher phenolic contents (Lowman & Box 1983) and corresponding lower grazing levels than their shade leaves. The physical conditions of temperature, wind and exposure to predators may be further deterrents to sun leaf grazing although these remain as yet untested. Sun leaves lost 9.4% and 13% leaf area in *C. apetalum* and *D. sassafras*, respectively, as compared to 35.3% and 16.3% in their shade leaves.

The monthly increments of leaf area losses differed slightly between sun and shade leaves (Fig. 4). In *D. sassafras*, the shade leaves underwent highest grazing pressures during November, 1 month earlier than did sun leaves; this time lag coincides with leafing phenology, however, since shade leaves emerged earlier and insects preferred

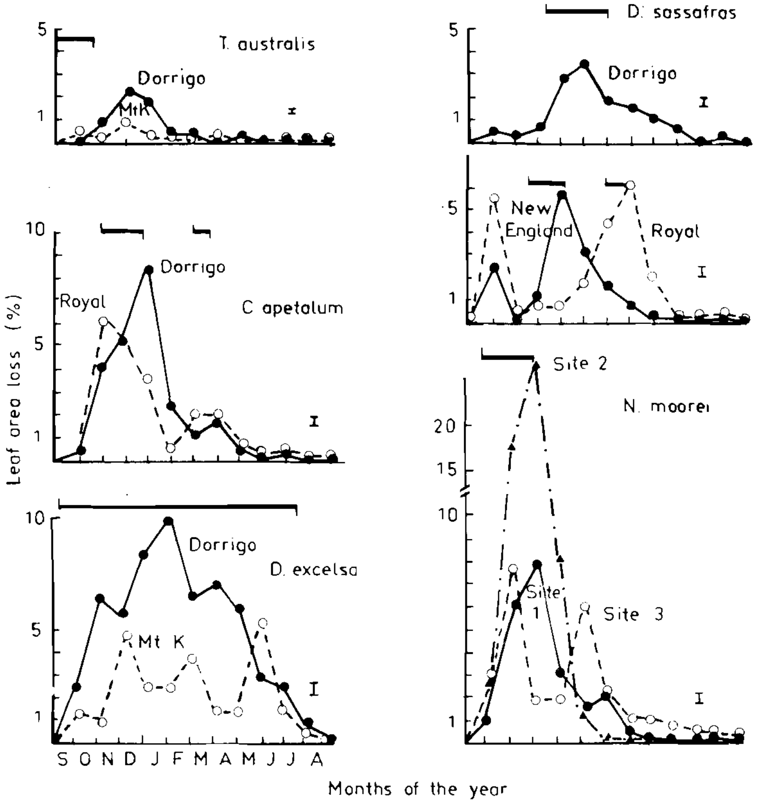

FIG. 3. Monthly increments of leaf material defoliated by insect herbivores in tree canopies of five species at several sites. Each point represents mean leaf area eaten per leaf per month expressed as a percentage of total leaf surface. Horizontal bars indicate a leaf flush; vertical bars are s.e.m.

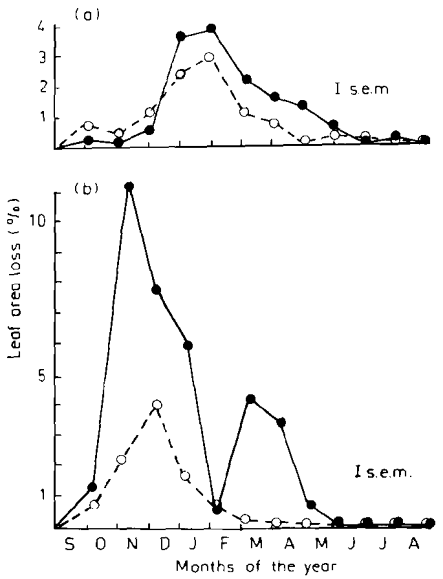

FIG. 4. Monthly increments of leaf material defoliated between sun (○) and shade (●) leaves of (a) *D. sassafras* and (b) *C. apetalum* expressed as mean proportion grazed per leaf each month. Shade leaves were more heavily grazed (see text) and defoliation was significantly more severe in months as follows (SNK rankings in ascending order, with statistically similar months in braces, brackets and parenthesis): *C. apetalum*: $F_{11,12}$ = 11.98, $P < 0.001$:
{July, June, May, August, [April, January, September, (March, February) December, November, October]}
D. sassafras: $F_{11,12}$ = 8.89, $P < 0.001$:
{August, June, July, October, May, September, April, November, March [February (December], January)}

young leaves (Lowman 1982b). Similarly, the shade leaves of *C. apetalum* show two defoliation peaks (November and February) which are times of peak leaf emergence for shaded portions of the canopy.

2. ***Height***. Three species exhibited differences in leaf size with height: *C. apetalum, N. moorei* and *D. sassafras*. All five species nonetheless, were monitored for herbivory at different height levels. *N. moorei, T. australis* and *C. apetalum* showed significant differences in herbivory rates at different canopy heights (Table 5).

D. sassafras had statistically similar grazing losses at 1 m, 5 m, and 15 m heights ($F_{2,72}$ = 1.87, n.s.). Mean leaf area losses were greater in leaves near ground level than above (30.4%, 21.3%, and 13%, ascending upwards in the canopy), but the range of proportions grazed from individual leaves was so variable that significance between groups was eliminated.

Insects generally preferred to graze leaves in the lower canopy. All three species that had statistically significant grazing levels at different canopy heights, exhibited decreases in grazing losses ascending the canopy (Table 5). Leaves located near ground level of *C. apetalum, T. australis*, and *D. excelsa* received more herbivory than in the upper canopy foliage (Table 5), usually at least twice the amount. This difference with height in the canopy may be partially an interaction between nearness to ground level (many insects appear to live near the ground) and light regime (shade leaves are more palatable).

The temporal changes in defoliation for *C. apetalum* leaves illustrate different monthly increments grazed at three canopy heights (Fig. 5). The lower leaves are grazed most heavily in October, whereas defoliation of the upper canopy peaks in December. This time lag reflects the canopy leaf phenology; shade leaves emerge first with progressive flushing up the canopy, and insects prefer to eat the young leaves.

TABLE 4. Variation in herbivory between sun and shade leaves of Australian rainforest canopies

	Herbivory loss (expressed as % leaf area missing)					
Species	Sun leaves	Shade leaves	$\bar{x}$	s.e.m.	F	Sign.
D. excelsa	32.5	—[a]	32.5	3.6		
T. australis	4.8	—[a]	4.8	0.6		
N. moorei	30.1	31.3	30.7	3.4	0.62	n.s.
D. sassafras	13.4	16.3	14.8	2.2	4.0	*
C. apetalum	9.4	36.3	22.4	2.3	28.3	†

[a] Leaves of this species grew *only* in the sun. n = 100 leaves per sample; significance levels: * $P < 0.05$, † $P < 0.001$.

TABLE 5. Variation in herbivory among Australian rainforest canopy leaves at different canopy heights

	Herbivory at different canopy heights (expressed as % leaf area lost)				
Species	Lower (0–3 m)	Middle (3–7 m)	Upper (>7 m)	F	Sign.
D. excelsa	42.6 >	*24.6*	*21.2*	12.7	‡
T. australis	7.9 >	4.2 >	1.8	10.6	†
N. moorei	*43.7*	*53.8*	*53.8*	0.8	n.s.
D. sassafras	*30.4*	*20.1*	*13.0*	1.86	n.s.
C. apetalum	36.3 >	*13.5*	*12.2*	4.13	*

Canopy heights with statistically similar herbivory are in italics. (Student Neuman-Keuls ranking tests). Degrees of freedom: 29 297; significance levels; * $P < 0.05$, † $P < 0.01$, ‡ $P < 0.001$.

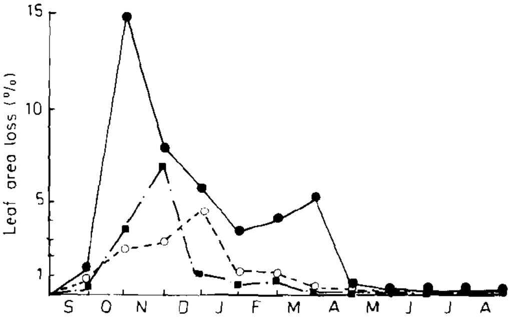

FIG. 5. Monthly herbivory losses of canopy leaves of *C. apetalum* at three canopy heights: low ● (0–3 m), mid ■ (3–10 m), and high ○ (> 10 m). Each point represents mean proportion of leaf area grazed per month per leaf.

3. Individuals — individual leaves, branches, trees and sites. The necessity of sampling large numbers of leaves throughout different spatial scales in order to obtain accurate estimates is illustrated in Table 6. It is often possible to obtain a small standard error with only a few leaves (e.g. 10 leaves of *C. apetalum* yields 10.2% herbivory with s.e.m. = 5.0), but it is unlikely that a small sample gives an accurate grazing level for the entire canopy (N.B. 10.2% for 10 leaves versus 26.7% for 100 leaves, the latter being more accurate).

TABLE 6. Herbivory losses in Australian rainforest canopy trees, illustrating levels of accuracy with different leaf sample sizes

	Number of leaves	Leaf area loss	s.e.m.
N. moorei	3	18.3	15.9
	10	25.0	12.3
	30	29.2	6.2
	50	28.9	4.6
	100	29.5	3.4
D. sassafras	3	23.3	12.0
	10	20.8	9.9
	30	21.6	6.4
	50	14.0	4.1
	100	14.4	2.5
D. excelsa	3	12.0	7.0
	10	27.7	12.2
	30	26.4	6.4
	50	25.2	4.4
	100	32.7	2.8
T. australis	3	0.33	0.3
	10	0.60	0.2
	30	1.47	0.8
	50	1.7	0.4
	100	2.5	0.4
C. apetalum	3	18.7	15.7
	10	10.2	5.0
	30	12.3	3.9
	50	16.9	3.9
	100	26.7	3.0

To better illustrate spatial variability on a small scale, Table 7 shows the leaf area losses among branches and individual trees of *N. moorei*. Adjacent leaves often have extremely different levels of grazing damage, and even branch to branch variability can be high. *N. moorei* had mean herbivory losses of 74%, 18% and 22% on three branches of one tree (site 1, tree 1, Table 7) which illustrates the necessity of sampling different branches throughout a tree canopy. Three sites exhibited different herbivory losses ranging from 19% to 38% and 39%, stressing the necessity to sample several sites in order to accurately estimate grazing of a species. The other four rainforest species also exhibited different mean grazing losses between sites, and different population levels of insect grazers (Lowman 1982c).

Temporal patterns of grazing between geographic regions (north-central and southern NSW) are illustrated in Fig. 3. Grazing intensities of most species were higher in the north-central (Dorrigo, New

TABLE 7. Variation in herbivory rates among branches, trees, and sites for *N. moorei* at New England National Park during the growing season of 1980

	Branch 1	2	3	$\bar{x}$
Site 1				
Tree 1	74.17	18.33	21.88	38.09
Tree 2	42.00	36.24	46.08	41.44
Tree 3	52.00	45.83	5.86	34.56
$\bar{x}$				38.03
Site 2				
Tree 1	60.07	8.69	12.42	27.06
Tree 2	56.89	11.20	50.89	39.66
Tree 3	47.33	66.83	40.10	51.42
$\bar{x}$				39.38
Site 3				
Tree 1	17.40	25.17	9.54	17.37
Tree 2	1.33	11.00	32.48	14.94
Tree 3	29.56	25.56	19.82	23.98
$\bar{x}$				18.76
Overall mean				32.06

Each branch was composed of 8-15 leaves, of both current and last year's leaf flushes. Leaf area was expressed as % grazed from total leaf area, with mean leaf size approximately 14.7 cm^2.

TABLE 8. Insect grazing in canopies of *Doryphora sassafras* from three Australian rainforest formations.

Site	Herbivory (% leaf area loss)	Species commonness proportion (%) site occupied by canopy)
Subtropical		
sun leaves	13.4	5
shade leaves	16.3	5
Canopy total	14.9	10
Warm temperate		
sun	17.6	10
shade	27.6	10
Canopy total	22.6	20
Cool temperate	12.3	14

England) sites than in the south-central (Royal, Mt Keira) ones probably because the northern region is closer to the centre of subtropical and warm temperate rainforest distributions, and presumably their associated insects would be more abundant.

D. sassafras is one of few Australian trees found in all three NSW rainforest formations; it attains canopy status in the subtropical and warm temperate sites, and occurs in the understorey of all three formations. Because species diversity within the three areas is very different and the relative proportions of *D. sassafras* also differs, it creates an opportunity to compare herbivory of one species with respect to its commonness. Herbivory of *D. sassafras* foliage was heaviest in the warm temperate site where it was most common (Table 8) and lowest in the cool temperate sites where foliage biomass was smaller and the trees widely dispersed. This supports Root's resource concentration hypothesis (1973), and represents its application to a long-lived, perennial species occurring late in succession.

Discussion

Discrete versus long term sampling

The amounts of leaf area loss measured by the two methods of sampling varied by a factor of 2–3 (Table 9). Long term sampling, whereby leaves were permanently marked and herbivory was measured over time and throughout different regions of the canopy, provided a more comprehensive estimate of grazing since leaves that were totally eaten could be accounted for as well as leaves only partially eaten. In evergreen forests where leaves remain on the tree for overlapping generations (not for one distinct season as in northern temperate hardwoods) and the microclimate is extremely variable among canopy levels, it is necessary to distinguish between populations or cohorts of leaves and measure the defoliation of each group through time.

In the literature, many field methods have merely involved discrete sampling whereby leaves are picked and measured for holes in leaf material collected (e.g. Bray 1961, 1964; Odum & Ruiz-Reyes 1970; Fox & Morrow 1983). This method may underestimate herbivory, however, since it does not include totally eaten leaves nor does it incorporate an accurate temporal component of grazing activities (Lowman 1984). Studies that employed discrete sampling in neotropical rainforests showed grazing levels of 7% (Odum & Ruiz-Reyes 1970), whereas more recent research that accounted for leaves totally eaten resulted in leaf losses approximately 3 times greater (21%, Coley 1982). A similar discrepancy of 2–3 fold resulted when discrete and long term sampling methods were compared in Australian rainforests (Lowman 1984). Studies of insect defoliation in eucalypts of Australian pastures are showing similar discrepancies when sampled by different methods (Lowman & Heatwole unpubl.). Discrete sampling is useful, however, to measure relative differences between leaf samples, and it may even approach the accuracy of long term samples when discrete collections are made repetitively and extensively.

This study examined herbivory solely in terms of canopy loss to the tree. Proportional losses of photosynthetic tissue in a tree's canopy provided the best expression of damage in a standard manner among species with different leaf sizes. Proportional losses, however, have limitations for estimating insect populations and for interpreting actual metabolic losses to the trees. First, leaf area loss reflects damage by foliage-feeding insects, but overlooks sap-suckers, stem borers, and other types of folivory. So, all herbivory levels reported here are underestimates of total insect damage. Secondly, percentage losses do not always indicate the actual amounts (cm^2) consumed by insects due to leaf size variability. (For example, 10% of a large leaf feeds more insects than 10% of a small leaf.) Third, if plant species have different inherent capacities for recovering from grazing, then measurements of grazing may not really reflect plant stress. For ex-

TABLE 9. Differences between two sampling methods for measuring herbivory rates in Australian rainforest trees (and between populations* of leaves within these canopies. $n = 200$ leaves unless otherwise stated

Leaf population	Sampling method for measuring herbivory rates (%)				
	Long term mean	s.e.m.	Discrete mean	s.e.m.	Discrepency ratio (L/D)
Toona australis — subtropical					
north-central	6.3	0.3	5.7	0.2	1.1
south-central	3.3	0.2	2.9	0.1	1.1
$\bar{x}$					1.1
Dendrocnide excelsa — subtropical					
north-central	32.5	2.6	16.5	1.0	2.0
south-central	15.5	1.4	8.0	0.9	1.7
$\bar{x}$					1.9
Ceratopetalum apetalum — warm temperate					
sun leaves	16.9	2.0	3.4	0.5	5.0
shade leaves	35.3	2.5	0.4	1.1	3.8
$\bar{x}$					4.4
Nothofagus moorei — cool temperate					
subsite 1 ($n = 500$)	22.5	2.1	11.7	1.0	1.9
subsite 2 ($n = 500$)	40.5	1.8	15.0	0.9	2.7
subsite 3 ($n = 150$)	30.3	3.0	13.6	1.4	2.2
$\bar{x}$	31.1		13.5		2.3
Dorhphora sassafras — cool temperate	13.6	1.8	12.0	1.2	1.1
subtropical					
sun leaves	13.4	2.0	4.4	0.7	3.0
shade leaves	16.3	2.2	6.4	0.7	2.5
warm temperate					
sun leaves	17.6	2.2	4.5	0.9	3.9
shade leaves	27.8	2.6	7.6	0.9	3.7
$\bar{x}$					2.6
Overall mean ration long term/discrete sampling difference					2.5

* Populations of leaves are defined as groups of leaves with significantly different morphological features (e.g. sun and shade leaves). For statistical data (ANOVA) determination of leaf populations, see Table 2.

ample, 20% loss to one tree may not be as severe as 20% loss to another, if they have different capacities for regenerating. The logistic problems of conducting controlled experiments to compare the effects of defoliation levels on large trees render it difficult to quantify these differences.

Another problem relating to the interpretation of grazing losses involves the type of tissue defoliated. If a tree loses half a young leaf (recorded as 50% leaf area loss), is this more or less detrimental than 50% loss of a mature leaf? In terms of canopy biomass, the areas are equivalent since the young leaf expands and the proportion missing remains 50% in both cases. However, the losses to plant metabolic processes may be different; consumption of a very old leaf may have a negligible effect on the tree since the leaf has lived most of its photosynthetically active life, whereas consumption of part of a young leaf may be a greater energetic loss since the tissue has not yet 'returned' the energy expended for its production.

To accurately monitor young leaf defoliation, field observations were sometimes necessary on a more frequent basis than monthly. I tried to spend long time periods in each site during periods of leaf flush to quantify defoliation and to distinguish it from wind damage, and senescence. In the rainforest understorey, where wind is infrequent and insects feed all night undeterred by flashlights, it was possible to learn to recognize many patterns of insect feeding behaviour. However, as explained in the methods, it is also possible that some leaves tallied as senesced were lost to stem borers or other unobserved phenomena.

Defoliation of moderate amounts of leaf tissue have been shown to stimulate growth in seedlings (Lowman 1982a), although the seasonality (Cremer 1973) and the intensity (Torres *et al.* 1980) of grazing will affect the tree's ability to recover. Similarly, the defoliation of tissues that were 'costly' for the tree to produce may represent a proportionally greater loss. In addition to the direct loss of photosynthetic tissue, herbivory may cause long term changes in reproductive fitness (e.g. seed production, Bentley *et al.* 1980; fruit-bearing branches, Janzen 1976), growth vigour (e.g. aspen and forest tent caterpillars, Churchill *et al.* 1964) or changes in grazing susceptibility of adjacent branches (Carroll & Hoffman 1980) or even individuals (Schultz & Baldwin 1982). Until the physiological effects of herbivory to plant metabolism are known, ecologists can only calculate the direct portions missing (i.e. leaf area losses) and speculate about the 'costs' to the plant in terms of reduced photosynthetically active tissue or changes in metabolic processes.

Relationships between plant defence and the behaviour of insect herbivores

Variability in herbivory rates between leaf populations reflects the adaptation of different resistance mechanisms amongst plants (Beck 1965; Visser & Mink 1982; and others). These may include differences in investment protecting leaf tissue, or intrinsic differences in abundance or feeding behaviour of insects in relation to distribution of the host plant (e.g. Burdon & Chilvers 1974 for eucalypts). For some species, the production of photosynthetic tissue represents a big investment, especially where leaves are long-lived or few in number. Plants have evolved characteristics that provide effective defence of leaves against early mortality (physical, chemical, nutritive, temporal, or spatial attributes), and these are well reviewed in the literature (e.g. Cates & Rhoades 1977).

The seasonality of insect herbivores is described in detail elsewhere (Lowman 1982b, 1982c; Selman & Lowman 1983). In general, two relationships between insect feeding behaviour and leafing phenology of Australian rainforest canopies were observed, both of which involved insect life cycles in close synchrony with the availability of young leaf tissue. The two underlying patterns were that of guild-feeding insects within intermittently or continuously growing canopies, and that of specialist feeders with synchronous canopy growth patterns.

Guild-feeding insects in intermittently or continuously growing canopies. In the subtropical and, to a lesser extent, the warm temperate rainforests, many tree species coexist with different but simultaneously active growth patterns. The production of new leaves in the canopy (albeit of different species) is continuous. This creates a spatially patchy but temporally continuous food supply; new leaves are not always available on the same tree but new leaves always exist somewhere in the canopy. Thus, for the insect capable of moving between the canopies of individual trees and of eating several species, such forests offer abundant and predictable food. In Australia, this pattern was observed for most herbivores in subtropical and warm temperate sites. I called them guild feeders, since they fed on similar but different rainforest leaf populations. They ate different species, but usually leaves that were similar in age and texture. This association parallelled the guilds of fish living in similar but different niches on coral reefs (Sale 1976, 1977). Guilds of reef fish may occupy slightly different heights in the water column or feed on different types of algae. Similarly, guilds of rainforest insects feed at different heights or different branches or in adjacent trees. Although there was a relatively high diversity of insects (like fish), they never appeared to compete; rather, their survival was a matter of chance in terms of success in locating a branch with leaves of palatable age, texture and chemistry. Insects in these guilds were not true generalists, however, since they exhibited preference for leaves of specific age, light regime, and texturally similar species. These insects had rather extensive lifespans as herbivores, often abundant for at least several months when young leaves were continuously available.

Specialist insects in seasonally growing canopies. The second pattern of insect-plant interaction was that of the specialist feeder, which fed exclusively on one species. For example, *N. moorei* dominated the cool temperate canopy, and its leafing pattern involved a synchronous rapid leaf flush in early spring. Most cool temperate herbivores fed voraciously during only one short period, and their life cycles were synchronized to tree phenology (Selman & Lowman 1983). Herbivores in the cool temperate rainforest were short-lived (usually 1–2 weeks) during the brief time of beech leaf flushing.

The relationship of host-specific insects with ephemeral leaves (e.g. *Novocastria nothofagi*, Coleoptera: Chrysomelidae), young beech leaves, or leaves of early successional species (e.g. *D. excelsa* and *Hoplostines viridipennis*, Coleoptera: Chrysomelidae), to generalists with predictable leaves (e.g. walking stick and mature leaves of many species) has been previously noted in other plant-insect studies (e.g. Rhoades & Cates 1976) but not often in perennial plant communities. It would appear advantageous to be a specialist in a rainforest canopy where one species and/or one growth phenology dominates, and a guild feeder ('generalist') in a diverse canopy where many growth phenologies and species exist. In the cool temperate rainforests, where beech forms a monospecific upper canopy, grazing by host-specific herbivores was relatively high. The slightly lower levels of herbivory in the diverse, subtropical forest may indicate effective spatial escape for a tree species as compared to single-species stands of beech; however, this remains to be experimentally tested.

It is suggested that studies of insect grazing levels should be conducted with reliable methods and with careful selection of habitat if the data are intended to assess an accurate level of insect impact for an entire habitat. Further, authors who cite literature without consideration of methods used, should be cautious about extrapolating the results of such defoliation studies to other systems. It appears that the levels of defoliation in Australian rainforests (~ 20%) may be higher than in the neotropics where defoliation is approximately 7% (but see Coley 1982). Until more extensive studies (including several canopy species and different canopy regions) have been completed in other rainforests, however, it is impossible to ascertain whether Australian herbivory levels are indeed higher.

Summary

Seven factors were isolated that contributed to variability in herbivory rates of rainforest canopy trees: leaf age, spatial scales, host species, canopy height, time, light regime and tree abundance. These factors also interacted to create additional variability among different portions of the canopy. Leaf age caused the most striking differences; herbivores preferred young over old leaf tissue, despite a proportionally greater amount of old leaf material within most canopies. Spatially, insects appeared to graze intermittently throughout the canopy, leaving some branches intact while defoliating others. Insects fed more extensively on the lower, shade leaves. Temporally, herbivory varied significantly among months in all species, albeit grazing was highly seasonal for *N. moorei* but rather continuous for *D. excelsa*. Overall annual grazing was different among species: 33% in *D. excelsa*, 31% *N. moorei*, 14% *D. sassafras*, 22% *C. apetalum* and 5% *T. australis*. Sampling artefacts may influence the accuracy of herbivory measurements. Long term observations provided the most accurate measurements, whereas discrete samples resulted in underestimated values, but may be useful for large scale comparisons or to show relative differences between species.

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APPENDIX 1. Tabulation of rainforest leaves measured by long term and discrete sampling

Species and site	Long term Trees (*n*)	Branches† (*n*)	Leaves (*n*)	Discrete Times sampled (*n*)	Leaves (*n*)
N. moorei					
New England National Park					
site 1*	4	30	704	6	180
site 2*	3	25	1003	16	480
site 3	3	9	260	9	270
Total			1967		930
D. sassafras					
Dorrigo National Park*	6	26	694	11	330
Royal National Park	3	9	151	15	450
Mt Keira*	3	9	170	10	300
Total			1015		1080
C. apetalum					
Dorrigo National Park*	4	12	190	11	330
Royal National Park*	3	21	395	14	420
Total			585		750
T. australis					
Dorrigo National Park*	3	9	99	3	90
Mt Keira	3	20	275	10	300
Total			374		390
D. excelsa					
Dorrigo National Park*	3	12	146		
Mt Keira	3	9	96		
Total			242		
Total			4183		3390

* Indicates that at least three canopy levels were sampled for all trees. † Original number only. (Most branches, particularly in the upper canopy, expanded laterally and subsequently comprised several branches.)

APPENDIX 2. Some insects associated with rainforest trees

Order	Family	Species	Feeding habits	Site	Time observed
	Some herbivores associated with *Nothofagus moorei*				
Coleoptera	Buprestidae	*Nascioides* sp.	?	New England	October
	Cantharidae	*Chauliognathus lugubris* (Fabrucus)	?	New England	May
		Heteromastix sp.	?	New England	November
	Cerambycidae	*Oricopis maculiventris* Lea	?	New England	Oct.–Jan.
	Coccinellidae	*Coccinella repanda* Thun.	polyphagous	New England	October
		Rhizobius sp 1, and sp. 2	?	New England	November
	Curculionidae	*Apion sp.* (trilobicolle group)	polyphagous	New England Lamington	Oct.–Jan.
		Myrmecoelus sp.	oligophagous	New England	September
		Aoplocnemus armipennis Lea	oligophagous	New England	December
		Cryptolhynchinae — gen? sp. 1, 2, 3	oligophagous	New England	Nov.–Dec.
		Aterpus tuberculatus Gyllenhal	?	New England	September
		Saccolaemus sp.	?	New England	September
	Scarabeidae	*Heteronyx* sp.	?	New England	Nov.–Jan.
		Diphucephala sp.	polyphagous	New England Barrington Tops	October
	Chrysomelidae	*Edusella* sp.	polyphagous	New England	Nov.–Dec.
		Monolepta sp.	oligophagous	New England	October
		Macrogonus ventralis Lea	?	New England	November
		Geloptera gen? sp. 1	monophagous	New England	September
		Longitarsus sp.	?	New England	November
		Novocastria nothofagi Selman	monophagous	New England Lamington Barrington Tops	Sep.–Feb.
Homoptera	Aphidadae	*Sensoriaphis furcifera*	polyphagous	New England	October
	Acanthosomatidae	*Panetius* sp.	?	New England	October
	Membracidae	nymphs?	?	New England	November
Lepidoptera	Lyonetiidae	*Bedellia* sp.	?	New England	September
		5–10 unknown moth larvae	?	New England	Sep.–Nov.
Phasmatodea	Phasmatidae	*Didymuria violescens*	polyphagous	New England	Sep.–March
	Insects associated with *Ceratopetalum apetalum*				
Coleoptera	Alleculidae	*Homotrysis* sp.	polyphagous	Dorrigo (NN)	Nov.–Jan.
	Chrysomelidae	*Edusella* sp.	polyphagous	Royal, Dorrigo	Nov.–Jan.
		Colaspoides sp. 1	oligophagous	Dorrigo	Oct.–Jan.
		Geloptera sp. 2	?	Dorrigo	October
		Rhyparida sp.	?	Dorrigo	October
	Coccinellidae	*Scymnus notescens* (Blackburn)	polyphagous	New England	October
	Scarabeidae	*Diphucephala* sp.	polyphagous	Barrington Tops, Dorrigo	October
	Curculionidae	*Perperus* sp. 1 & 2	oligophagous	Royal, Dorrigo	Oct., Dec.
		Leptopius puellaris (Pascoe)	?	Dorrigo	Nov.–Dec.
		Diabathrarine (Zimm ms.)	?	Dorrigo	Nov.–Dec.
		Meriphus tuverculatus	?	Royal	December
		Brachyderinae (gen? sp?)	oligophagous	Dorrigo	November
	Lagriidae	*Lagria* sp.	oligophagous	Dorrigo	September
Phasmatodea	Phasmatidae	*Didymuria violescens*	polyphagous	Dorrigo, Royal	Sep.–June

Order	Family	Species	Feeding habits	Site	Time observed
	Herbivores associated with *Doryphora sassafras*				
Coleoptera	Chrysomelidae	*Edusella* sp.	polyphagous	Dorrigo, Royal, New England	November
		Halticinae gen? sp?	?	Lamington	January
	Coccinellidae	*Egleis edwardsi*	polyphagous	Royal	September
	Curculionidae	*Myrmecoelus* sp.	oligophagous	New England	September
		Peropterus ellipticus Pascoe	oligophagous	Dorrigo, Royal	September
		Peropterus inocuus Boheman	oligophagous	Royal	August
		Apion sp. (trilobicolle gp.)	polyphagous	Dorrigo, Royal, Mt Spec.	Aug., Sep.–Jan.
		Tychiinae sp?	?	Dorrigo, New England, Barrington Tops	October
		Leptopius gladiator (Lea)		Dorrigo	September
		Brachyderinae (gen. sp. undescr.)	?	Dorrigo	November
		Aoplocnemus armipennis Lea	?	New England	December
		Cryptohynchinae (gen? sp?)		New England	Nov.–Dec.
		Erichininae gen. 1, 2	oligophagous	Dorrigo	November
		Belidae sp.	?	New England	November
	Scarabeidae	*Diphucephala* sp.	polyphagous	New England, Dorrigo, Barrington Tops	October
	Lagriidae	*Lagria tomentosa* Fabricus	?	Royal	December
Phasmatodea	Phasmatidea	*Didymuria violescens*	polyphagous	New England Dorrigo, Royal	Sep.–July
	Herbivores associated with *Dendrocnide excelsa*				
Coleoptera	Chrysomelidae	*Hoplistines viridipennis*	monophagous	Dorrigo Lamington	Sep.–July; Spring
		Nisotra sp.	?	Davies Creek, N.Qld	August
Hemiptera	Dictyopharidae	*Thanatodictya* sp.	?	Davies Creek, N. Qld	August
Homoptera	Aphididae	*Sensoriaphis furcifera*	polyphagous	Dorrigo	November
Lepidoptera	Hepialidae	*Aenetus eximus*	?	(Australian Museum records)	
		A. scotti	?	(Australian Museum records)	
Phasmatodea	Phasmatidae	*Didymuria violescens*	polyphagous	Dorrigo, Mt Keira	Oct.–Jan.
	Herbivores associated with *Toona australis*				
Coleoptera	Melyridae	*Helcogaster* sp.	?	Dorrigo	September
	Curculionidae	*Apion* sp. (trilobicolle group)	oligophagous	Dorrigo, Mt Keira Davies Creek, N. Qld.	Aug.–Jan.
Homoptera	Aphidadae	*Sensoriaphis furcifera*	polyphagous	Dorrigo, Mt Keira	Oct.–Dec.
Lepidoptera		*Hypsiphyla robusta*	monophagous	Records: Francis 1951	