Chapter 16

The impact of herbivorous insects on Australian rainforest tree canopies

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Summary

The leaf-growth dynamics of Australian rainforest tree canopies were studied over a five-year period, to determine the patterns (if any) that existed in growth, mortality, and other aspects relating to phenology and productivity of this plant community. Representative species were selected within each of the three major rainforest formations of New South Wales. These included *Nothofagus moorei* and *Doryphora sassafras* in cool temperate rainforest; *D. sassafras* and *Ceratopetalum apetalum* in warm temperate rainforest; and *Dendrocnide excelsa*, *Doryphora sassafras*, and *Toona australis* in subtropical rainforest. Because herbivory appeared to have such a profound effect on the survival of rainforest leaves, further investigations were conducted on this aspect of canopy growth dynamics, including herbivore abundance, diversity, and also examination of possible physical and chemical defences of leaves.

Several factors were observed that led to variability in herbivory rates within different parts of the canopy: light regime, species, age of leaf, height of leaf in canopy, and sometimes individual tree or site. These factors were examined for each of the five species, with the following results. Sun leaves were less heavily grazed than shade leaves, and also had greater tannin and phenolic contents, and greater toughness values of leaf tissue. Young leaves were significantly more intensively grazed than old leaves; for example, approximately 51 per cent leaf-area losses were experienced by young *N. moorei* leaves, compared with less than 1 per cent losses to old leaves. Leaves located nearer to ground level suffered higher grazing, although this may be in part an interaction with light regime. Species had variable leaf-area losses from grazing: 5 per cent *T. australis;* 15 per cent *D. sassafras;* 22 per cent *C. apetalum;* 31 per cent *N. moorei;* and 33 per cent *Dendrocnide excelsa.*

The consequence of this fairly high turnover of leaf material to insect herbivores, especially in relation to decomposition, are compared among the different rainforest formations, and with other plant communities.

Introduction

The effects of primary consumers on forest trees are difficult to quantify (review in Kulman 1971). Herbivory is known to lower primary productivity (Mattson and Addy 1975), although moderate grazing has also stimulated growth recovery in annuals (Jameson 1963; Hodgkinson 1974; Torres et al. 1980) in some cases. Grazing rates in most forest communities have been estimated at 3–10 per cent. This includes northern temperate hardwood forests (Bray 1961, 1964), *Liriodendron* woods (Reichle and Grossley 1967); European beech forests (Nielson 1978); and neotropical rainforest (Odum and Ruiz-Reyes 1970; Stanton 1975). Two notable exceptions to this moderate rate include Australian communities: eucalypt woodlands where 20–75 per cent leaf-area losses have been reported (Kile 1974; Morrow 1977; Journet 1981) and Australian coral cay vegetation where up to 30 per cent losses were observed (Heatwole et al. 1981).

It is often assumed that insect herbivores have a negligible effect upon the lush Australian rainforest canopies, especially in comparison to the obvious effects of pests on sclerophyll plants. No studies have been conducted yet for Australian rainforest to test whether grazing levels are as high as in other Australian plant communities, or whether herbivory rates are more similar to the moderate consumption measured in neotropical rainforests. Close observations of the entire canopy of individual trees are required to quantify the grazing and defoliation activities in rainforests.

In 1979, a long-term research project was commenced, formulated around questions designed to eliminate several obvious, major gaps existing in the present literature on rainforest canopies. In particular, the biological aspects of phenology, longevity, herbivory, and population dynamics of leaves have not been examined for variability at several spatial scales: within canopy levels, among individual trees, between species, and among rainforest formations. Sampling among these different levels was facilitated by ropes and climbing gear. In essence, the leaves in a rainforest canopy can be viewed as a population and examined for growth, survivorship, and mortality in a similar manner as a zoologist views a population of animals. More specifically, the following questions were addressed:

i. What are the patterns of leaf dynamics within and among Australian rainforest trees, and what factors affect these growth patterns?
ii. What are the rates of turnover of leaf material to both herbivore and decomposer pathways, and how do grazing activities in the canopy vary on spatial and temporal scales?
iii. Ultimately, how much leaf material exists in a mature rainforest canopy at any one point in time?

The details of this research are listed elsewhere (Lowman 1983), but the impact of herbivory on the rainforest canopies is summarised here.

Site and species description

At least two representative sites of each of the three major rainforest types found in New South Wales (subtropical, warm and cool temperate) were selected for field

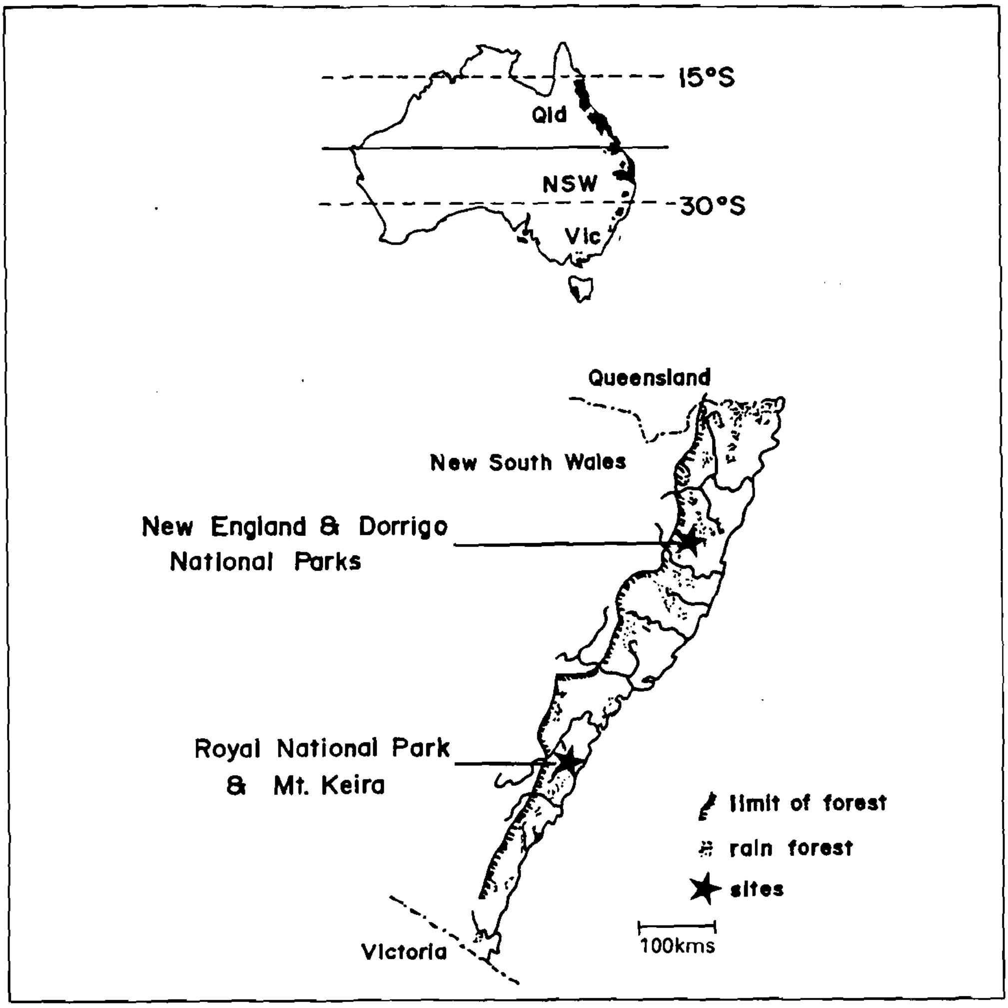

Figure 16.1 Location of study sites. Above: map of Australia showing distribution of rainforest discontinuously down the east coast. Below: map of New South Wales coast with northern sites (New England and Dorrigo National Parks) and southern sites (Royal National Park and Mt Keira)

work. The replication of sites facilitated comparisons of canopies both within and between rainforest types.

Warm temperate rainforest sites were located in Royal National Park and Dorrigo National Park (Never Never region); cool temperate in New England National Park (three isolated areas were studied within the Park to provide replication); and subtropical in Dorrigo National Park and Mount Keira (see Figure 16.1). All areas were relatively undisturbed, with well-developed canopies that were structurally conducive to the research methods of climbing for observations. Further information on the study areas is listed elsewhere (Lowman 1983).

Five species were chosen for close observation and field experimentation, since it was not logistically feasible to examine leaf growth dynamics throughout an entire rainforest canopy. The species were selected with respect to several criteria: representativeness of one of the three rainforest types under examination; leaf morphological characteristics that may be of particular interest to plant–insect interactions (e.g. presence of hairs or heavy cuticle); or variability of growth patterns (e.g. deciduous, evergreen). It was hoped that a range of species characterising different aspects of these criteria would represent the variability in leaf growth patterns existing in Australian rainforests. The five species included:

1. *Ceratopetalum apetalum* D. Don (coachwood) is a fairly common Australian warm temperate forest tree that ranges from Milton, New South Wales to the Queensland border. It often forms pure stands on poor, sedimentary soils, especially in the Dorrigo Plateau and the Hastings River areas, where it is an important timber species. Its straight, pale grey, smooth trunk extends to 30 metres in height, and may have short buttresses. The canopies often appear red in November–December after flowering, when the calyx lobes enlarge and turn colour before shedding.
2. *Doryphora sassafras* Endl. (sassafras) extends from the Victorian border to southern Queensland, and grows in all three New South Wales rainforest formations: subtropical, and warm and cool temperate. It occurs on basaltic soils as an understorey to Antarctic beech or in association with subtropical species; or on poorer, sedimentary soils with coachwood. It has straight, unbuttressed, dark trunks extending up to 42 metres. The white flowers are very obvious in the canopy during April–July or as late as November.
3. *Dendrocnide excelsa* (Wedd.) Chew (stinging tree) occurs in subtropical, dry and littoral rainforests from Tathra, New South Wales to Imbil, Queensland. Its fast, opportunistic growth pattern enables it to colonise small tree-fall gaps or more extensively cleared areas. But, in addition to regenerating immediately, it can also persist and occupy canopy status in subtropical stands, where it extends up to 40 metres. The wood is of no economic use, being very soft and light, and the creamy trunks have fluted buttresses. The trees are monoecious and the small, yellowish-green flowers occur during November–April. Stinging trees are renowned for their abundance of small stinging hairs that cover leaf surfaces and petioles, and impart a chemical and physical sting when brushed.
4. *Nothofagus moorei* F. Muell. (Antarctic beech) is distributed in cool temperate rainforests, usually above 600 metres in New South Wales, in the headwaters of the Hastings, Macleay, Bellingen, and Barrington rivers and on the McPherson and Tweed ranges. Beeches grow to 30 metres with crooked, dark, moss-covered trunks; they form single-species stands in these moist, montane sites. Trees are monoecious, and catkins form from August–December.
5. *Toona australis* (F. Muell) Harms (red cedar) is synonymous with rainforest timber history in Australia, because its red, durable wood was most highly sought by loggers. Although many areas have been extensively logged out, the range of cedar extends from Milton, New South Wales to McIlwraith Range, north Queensland. It grows in both subtropical rainforests on rich basaltic soils, and warm temperate rainforests with alluvial, sedimentary soils. The brown trunks grow to 45 metres and may have buttresses. Cedar is one of the few deciduous Australian rainforest trees. Its white flowers are very conspicuous in the canopy during September–November, since flowering coincides with the time of leaf emergence.

The most important criteria implicated in selection of these five species are:

i. coachwood—predominant in warm temperate rainforest and important economically;
ii. sassafras—found in all three rainforest formations;
iii. stinging tree—canopy-dominant in subtropical rainforest, and unique leaf morphological characteristic (stinging surface, hairs);

iv. Antarctic beech—dominant in cool temperate, forming naturally-occurring monospecific rainforest communities; and
v. red cedar—deciduous, and canopy-dominant in subtropical rainforest.

Field methods

Branches and individual leaves along the branches were permanently marked in order to conduct quantitative observations on leaf growth dynamics. Leaf-monitoring stations were established which consisted of at least three branches in a section of the canopy. The stations were selected randomly but with respect to the different sections of the canopies as defined in terms of various environmental factors.

Branches were marked initially during February–April 1979, well before the spring flush for that year (September–October). Leaves were numbered sequentially from the base upwards, with branches usually consisting of eight to fifteen leaves. Black waterproof Pentel pens were used to inscribe numbers on the adaxial leaf surface. The ink usually lasted up to one year before fading, in which case the numbers were remarked. The ink was not considered an artifact of sampling, since it did not result in mortality or deformation of any sort, 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 hyphenate 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 conducted, and branches were checked for leaf emergence, herbivory, senescence, tearing, desiccation, epiphylly, or any other aspect of leaf-growth dynamics.

In the event of herbivory, leaves were traced with their hole areas marked, and measured in the laboratory using an area meter (Lambda Model 300) to determine the amounts removed. Complete defoliation was distinguished from natural senescence by observation; older leaves that remained intact for several years and suddenly disappeared were recorded as having senesced; younger leaves in which holes increasingly appeared over several months during times of herbivore activity and disappeared while still young were recorded as defoliated.

In some cases, it was necessary to establish leaf-monitoring stations in the upper canopy. For initial samples, shotguns were used, but this destructive sampling is of limited value for any long-term data collection on leaf growth or herbivory. Instead, two additional methods were used that enabled establishment of permanently-marked sites in the upper canopy similar to the leaf-monitoring stations in the lower canopy: ladders and technical climbing hardware.

Long-term sampling—changes in leaf area missing per leaf were measured monthly on several hundred leaves for each of the five species using the area meter and leaf tracings.

For each species (or leaf population), the mean monthly increments eaten by herbivores were expressed as proportions of the total intact (or potential) leaf area (PLA), calculated by:

$$1.00 - \frac{\text{ALA}}{\text{PLA}} = \%\ \text{leaf area eaten.}$$

ALA (actual leaf area) is the leaf area remaining after the insects have defoliated it.

The annual herbivory rate simply represented cumulative proportions eaten during 12 months (e.g. a beech leaf may have lost 5 per cent leaf area in September, an

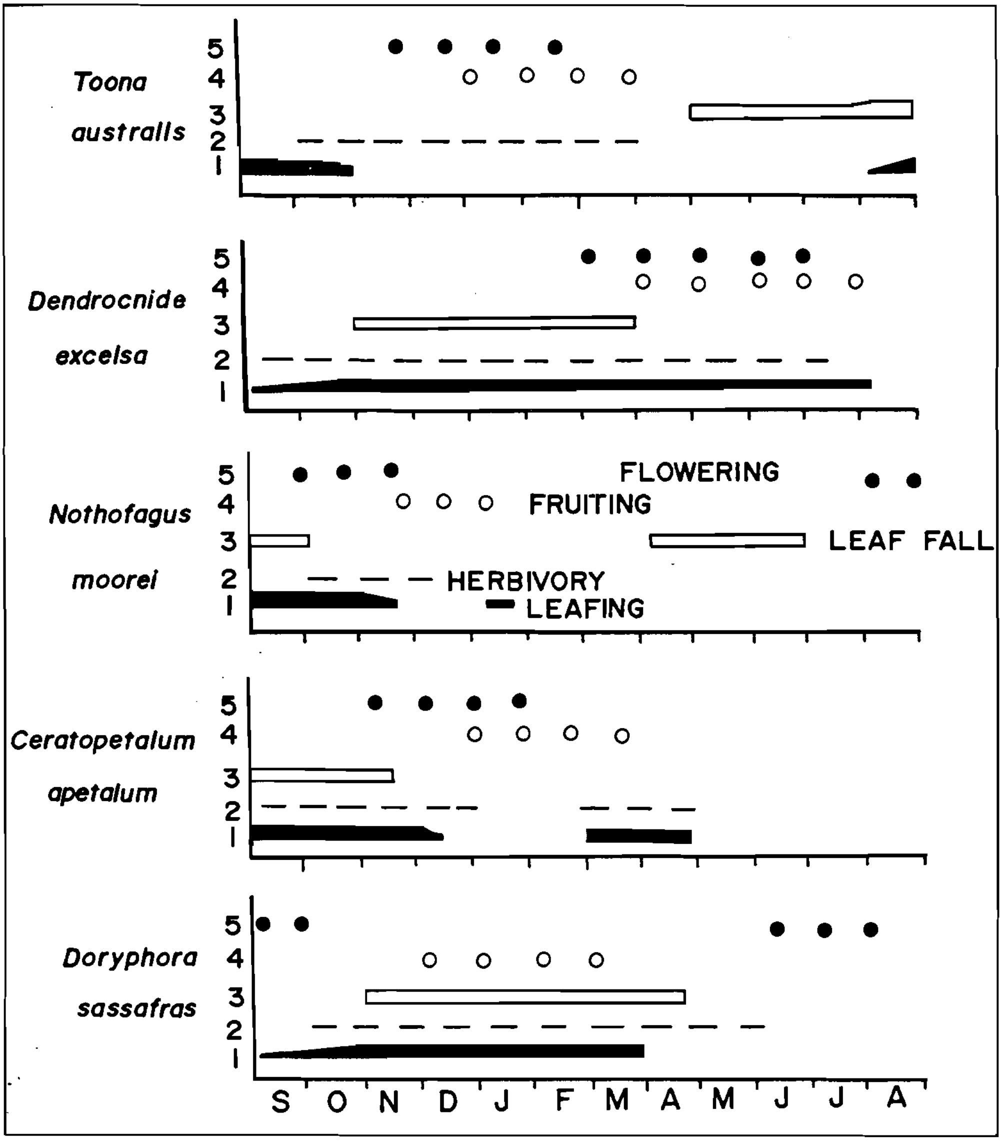

Figure 16.2 Phenological patterns summarised for five Australian rainforest trees, as observed in forests of New South Wales. From top to bottom of each chart symbols indicate: 5, flowering; 4, fruiting, 3, leaf fall, 2, herbivory; 1, leafing

additional 10 per cent in October, and nil per cent during the remaining 10 months, giving an annual herbivory rate of 15 per cent).

Results

The main phenological ptterns of rainforest tree canopies are illustrated in relation to herbivory (Figure 16.2). In most cases, insect defoliation coincided with leaf emergence, due to the preference of herbivores for young leaves. The overall herbivory patterns are listed by species.

1. *Dendrocnide excelsa*. Removal of leaf area by herbivores occurred throughout the year (except August) but with the heaviest defoliation during summer (November–February), the main leafing period (i.e greatest abundance of new food available to insects). The canopies lost approximatley 5 per cent leaf area per month, an extremely high rate (Figure 16.3a, b). Temporal variability in herbivory was statistically significant, with the heaviest grazing during January. Mean annual cumulative rate of loss per leaf was 32.5 per cent (88.8 cm^2) in Dorrigo and 15.5 per cent (42.5 cm^2) in Mount Keira (based on leaf longevities listed above and mean life size of 273.1 cm^2).

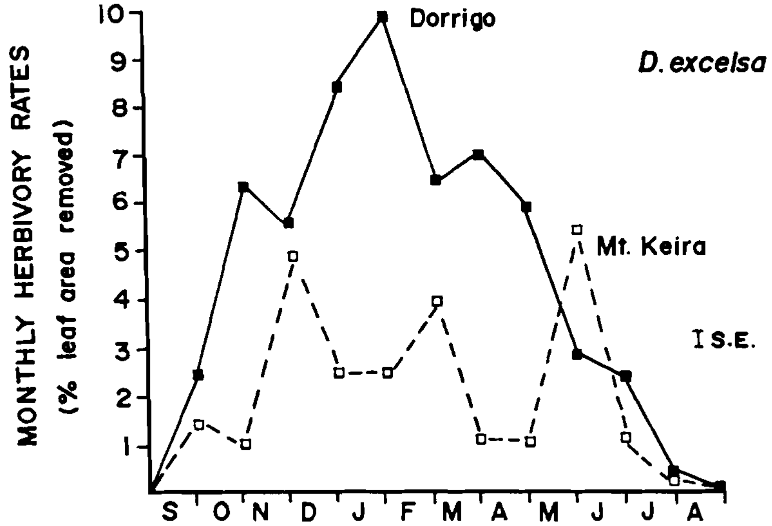

Figure 16.3a Monthly herbivory rates for leaves of *D. excelsa* at two sites, Mount Keira and Dorrigo National Park, expressed as mean proportion grazed per leaf each month

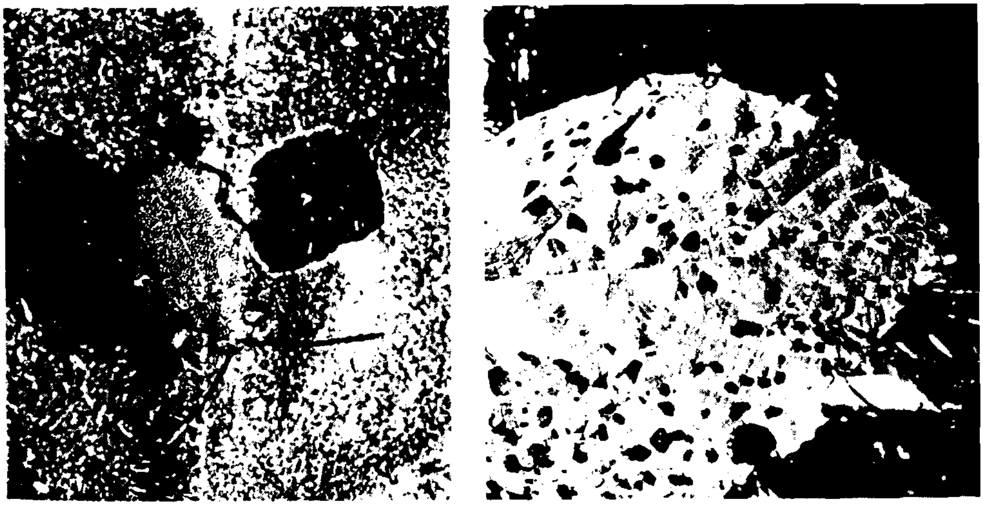

Figure 16.3b The host-specific chrysomelid beetle *Hoplostines viridipennis* on the surface of a *D. excelsa* leaf (left), and a mature *D. excelsa* leaf with the characteristic grazing pattern of the beetle (right)

2. *Toona australis.* Despite their soft, fairly mesomorphic tissue, cedar leaves suffered little herbivory, especially compared with neighbouring canopies of other rainforest trees (Figure 16.4). This suggested the presence of effective leaf defences such as secondary compounds (see Lowman and Box 1983). Mean leaf area loss to herbivores was 6.3 per cent (s.e. 1.17) in Dorrigo and 3.3 per cent (s.e. 0.37) in Mount Keira. The highest grazing level occurred in November but was only 2.25 per cent, less than half the mean monthly rate for *D. excelsa.*

Monthly variability in herbivory was just significant with most grazing occurring in November and December. Most of the leaf areas missing were small patches caused by aphids, the major herbivores observed over two years. The aphids are sucking insects, and do not directly remove leaf tissue; but their feeding spots usually turned brown or yellow, desiccated, and fell out, thereby appearing similar to damage from foliage-feeders. Other herbivores were observed less frequently, usually during the few weeks of cedar leaf emergence.

3. *Nothofagus moorei.* Insect herbivory was the major cause of early leaf mortality in beech canopies, with frequently more than half of a new flush entirely grazed. The leaf area removed comprised 31 per cent of the canopy annually (Figure 16.5a), although this overall rate varied considerably with several factors: time (among months and years); space (between branches, individual trees, canopy heights [Figure 16.5b], and sites); and age of leaf tissue. Leaves lost approximately 54 per cent leaf surface area during their first year and only 0.22 per cent during their second year. These factors were examined by comparing different subsamples within the beech leaf-monitoring studies, and are described in greater detail elsewhere (Selman and Lowman 1983).

4. *Ceratopetalum apetalum.* Herbivory resulted in annual mean leaf-area losses of 21.3 and 24 per cent in Royal and Dorrigo, respectively. These rates were not statistically different ($F_{1,\ 98}$ = 0.26, n.s.). Peaks in herbivory activities reflected the leaf emergence patterns at the two sites (Figure 16.6), since the young, emerging leaves were most heavily consumed by insects. The highest herbivory occurred during spring (October–November in Royal) with a one- to two-month delay in Dorrigo due to the later

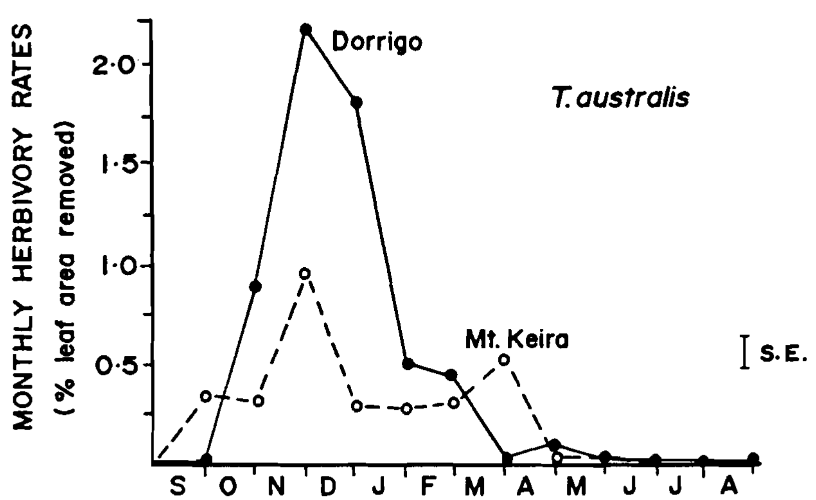

Figure 16.4 Monthly herbivory rates for leaves of *T. australis* at two sites, Dorrigo National Park and Mount Keira, expressed as mean proportion grazed per leaf each month

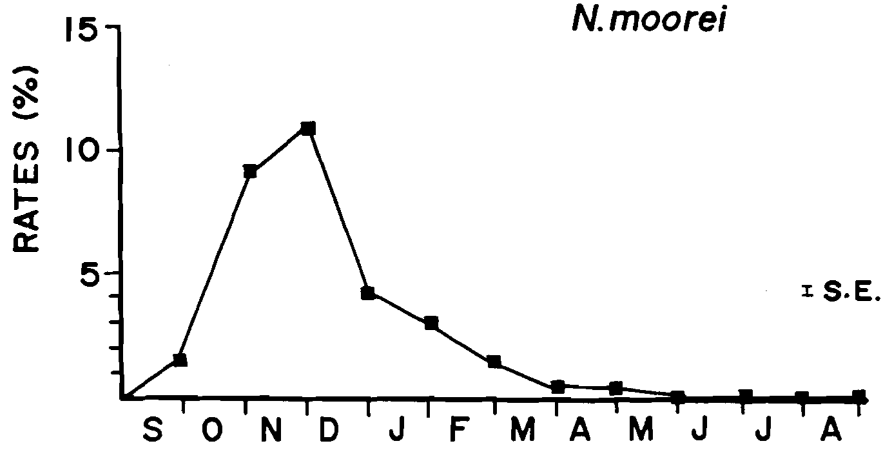

Figure 16.5a Monthly herbivory rates for leaves of *N. moorei* in New England National Park, expressed as the mean proportion grazed per leaf each month

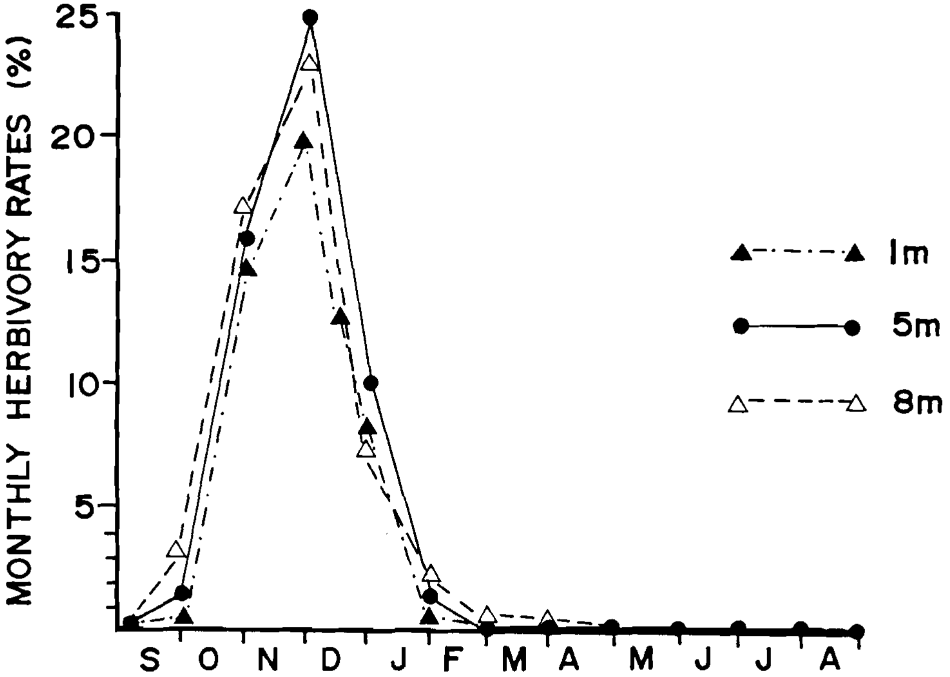

Figure 16.5b Monthly herbivory rates for leaves of *N. moorei* at three heights, 1 m, 5 m, and 8 m, expressed as mean proportion grazed per leaf each month. Grazing was not significantly different among heights ($F_{2.72}$ = 0.797, n.s.)

budburst there. A second, less significant peak occurred during late summer (February in Royal, and March in Dorrigo) after the second flush. Herbivore activities varied in different months, with the heaviest grazing occurring during October at Royal and in December at Dorrigo. Herbivory was examined for differences with respect to light (sun versus shade) with losses greater in the shade than sun: 35.3 per cent versus 9.4 per cent grazing rates ($F_{1,\ 98}$ = 28.31, $p<0.001$). Shade herbivory showed a bimodal

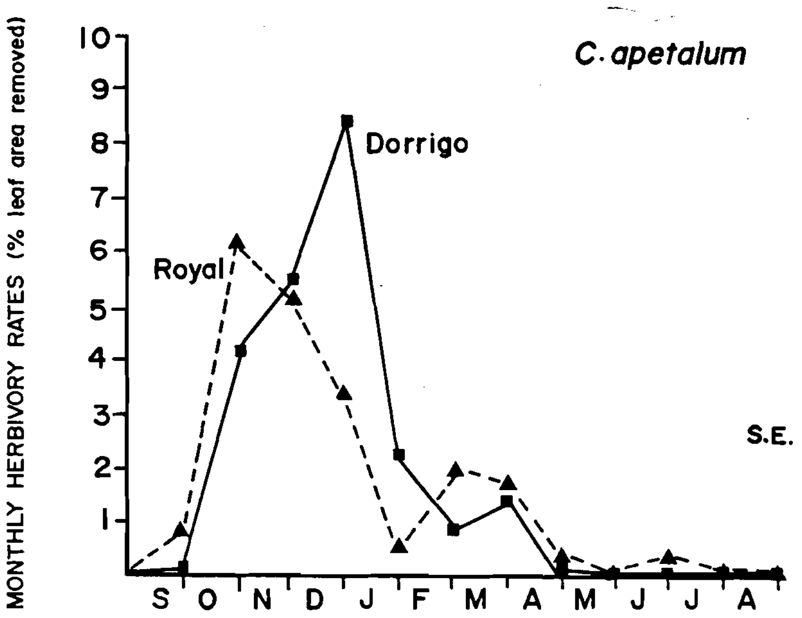

Figure 16.6a Monthly herbivory rates for leaves of *C. apetalum* at two sites, Dorrigo and Royal National Parks, expressed as mean proportions grazed per month. Herbivory was significantly different among months: Royal ($F_{11.12}$ = 11.98, pv 0.001), Dorrigo ($F_{11.12}$ = 8.75, pv 0.001)

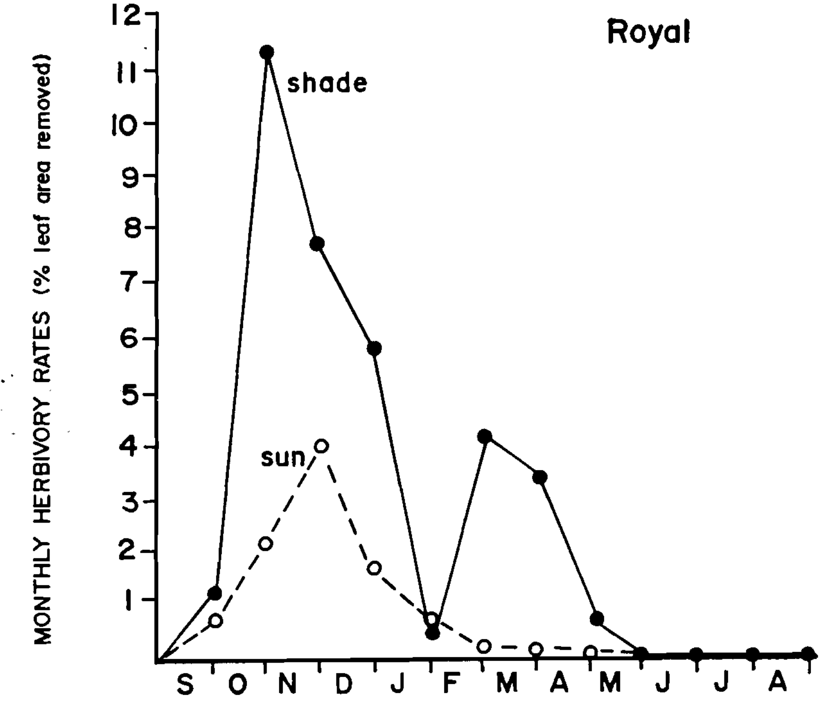

Figure 16.6b Monthly herbivory rates between sun and shade levels of *C. apetalum* in Royal National Park, expressed as mean proportion grazed per leaf each month. Shade levels were more heavily grazed (see text)

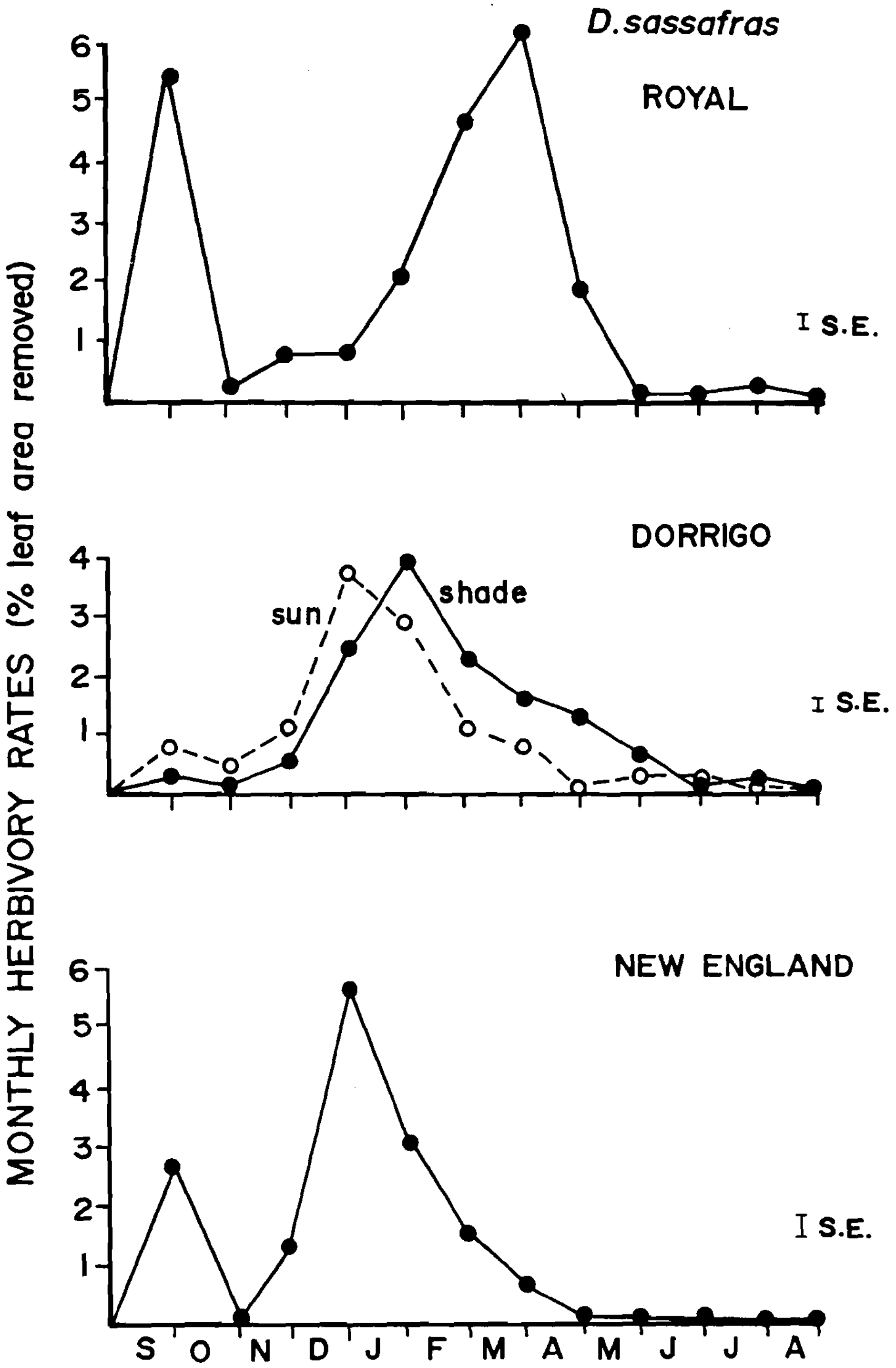

Figure 16.7 Monthly herbivory rates for leaves of *D. sassafras* in three sites: top to bottom, Royal (warm temperature), Dorrigo (subtropical) and New England (cool temperature) National Parks, expressed as the mean proportion grazed per leaf each month

temporal pattern (similar to the overall herbivory rates) while sun-leaf herbivory only exhibited one peak during November (sun-leaf emergence occurred only during spring). An analysis of herbivory at three heights in Royal (1, 10 and 15 metres) showed a significant difference between one metre and the upper heights ($F_{2,\ 72} = 4.13$, $p<0.05$). It is difficult to distinguish between the effects of light and height, however, since the lower leaves are invariably located in more shaded conditions. Insects appeared to prefer shade-leaf tissue which also suggested a preference for near-ground leaves; whether this was a consequence of nearness to ground or merely the palatability of shade-leaf tissue is not clear. It is necessary to monitor shade leaves located in the upper canopy to test this.

5. *Doryphora sassafras.* There was no significant difference in cumulative annual herbivory rates of sassafras canopies among the three sites ($F_{2,\ 117} = 0.55$, n.s.) with an average leaf-area loss of 16.6 per cent. Although grazing rates were slightly different between sites, the variability of proportions missing within sites was so high (between 0 and 100 per cent per leaf), that it resulted in a non-significant variance between sites as well. Insect grazing was statistically seasonal in the subtropical rainforest with one distinct annual peak, whereas grazing seasonality was less evident in the warm and cool temperate habitats that exhibited bimodal patterns (Figure 16.7).

Herbivory in shade- and sun-leaves were compared in Dorrigo, where the dense subtropical canopy created the greatest differences in light levels. There were significantly greater herbivory rates in shade leaves than sun, 16.3 versus 13.4 per cent ($F_{1,\ 58} = 5.89$, $p<0.05$). This difference is discussed elsewhere in relation to leaf chemistry (Lowman and Box 1983).

Discussion

Within the growth patterns observed, herbivory was critical in affecting leaf survival. Six factors were isolated that contributed to variability in herbivory rates: leaf age, space, tree species, time, light regime, and sampling method. These factors also interacted to create additional variability among different portions of the canopy. As leaves aged, they changed in chemical toxicity and in toughness (Lowman and Box 1983); this greatly limited the consumption of beech and coachwood leaves, but not of stinging tree leaves. On a spatial scale, there appeared to be an element of chance in herbivory: insects did not actively select leaves at specific heights or branches; instead, they appeared to graze at random, leaving some branches intact, apparently undiscovered by herbivores (see Lowman 1982). Temporally, herbivory varied on a monthly basis with all species, but more so for beech than for stinger. Rates of grazing differed between species: higher in stinger, followed by beech, coachwood, sassafras, and cedar, respectively (Table 16.1). And lastly, artifacts of sampling methods resulted in different measurements of herbivory rates. Long-term observations provided the most accurate measurements, while discrete, harvested samples always underestimated herbivory and were perhaps most useful for large-scale comparisons of relative differences between species. Of the six factors examined, leaf age caused the most striking differences: herbivores preferred young over old leaves, despite a proportionally greater abundance of old leaves within most canopies.

One major question that arises from this work concerns the higher rates of herbivory apparent in Australia than in other continents. Losses of 10–75 per cent in Australian eucalypt (Carne 1966; Morrow 1977; Journet 1981), up to 30 per cent in Australian coral cay vegetation (Heatwole et al. 1981), and 15–31 per cent in

Table 16.1 Variation in herbivory among Australian rainforest canopies

Species	*Mean herbivory rate (% leaf area consumed)*
Dendrocnide excelsa	32.5
Toona australis	4.8
Nothofagus moorei	30.7
Ceratopetalum apetalum	
sun	9.4
shade	35.3
Doryphora sassafras	
sun	13.4
shade	16.3
*Formations**	
Subtropical	14.6%
Warm temperate	22.0%
Cool temperate	26.0%

* See Lowman (1983) for explanation of calculation techniques.

rainforests (this study) are much higher than the losses of 3–10 per cent that are typical for American and European studies. There are two possible explanations for this major difference, one relating to differences in absolute numbers of herbivores and one relating to artifacts of sampling between studies.

Firstly, it is possible that herbivorous insects are simply more abundant in Australia compared with America, Europe, and Asia. This is certainly true for abundance of ants (Morton, personal communication); and has been suggested to explain the heavy grazing in eucalypts (Morrow, personal communication). The isolation of Australia may have gradually led to a different balance of numbers of organisms, especially herbivores. For example, it appears that coleoptera (especially Curculionidae) may be more common in Australian rainforests than in South American (Langenheim, personal communication). It is also conceivable that insectivorous birds are less common in Australia, thereby leading to greater insect abundance. A survey of Australian bird families (Kikkawa and Webb 1967) shows 23 per cent tree-feeding insectivorous species, but only 6 per cent among rainforest species (although this rises to 35 per cent when ground-feeding insectivores and onmivores are included). In contrast, Orians (1969) found 46 per cent among seven lowland and montane rainforest sites in Costa Rica ('insectivorous birds' including his categories of 'gleaning on trunks and branches', 'gleaning on leaves for insects', 'hovering for insects'; these most closely correlate with Kikkawa and Webb's category of tree-feeding insectivorous species).

A survey of Malayan rainforest mammals (Harrison 1962) cited 51 per cent as insect-feeding. Although a similar comparison for species of Australian rainforest mammals does not exist, it is unlikely that Australia has a similar high proportion, once again suggesting the possibility of higher herbivorous insect survivability here. Both studies, however, expressed their results in number of species (i.e. diversity), whereas abundance of each species (especially the insectivores) would be a better indicator of insect biomass removed by birds or mammals. A more extensive comparison between Australia and another continent of numbers of insect-eaters in specific forest areas would be of great interest.

Secondly, herbivory levels may *appear* to vary between habitats and continents, but only as a consequence of the methods employed by different ecologists. For example, the use of long-term and discrete sampling techniques caused a two- to three-fold discrepancy in measurable leaf-area losses (Lowman 1984).

As with most research in rainforests, the results perhaps stimulate more questions than they answer. The factors leading to variability in rates in herbivory—leaf age, species, time, space, light—all interact to create a wide latitude of effects on different sections of canopy. The seasonal patterns of herbivory have been defined, establishing a framework for further research in this region. For example, detailed measurements of the photosynthetic rates of leaves of different populations within the canopy would enable the modelling of productivity in these canopies. More extensive observations of insect-feeding preferences, particularly guild-feeders in the complex subtropical canopy versus specialists in the nonspecific canopy, will lead to understanding of plant–insect chemistry and grazing behaviour. Further studies of herbivory among rainforests of different species-richness will promote better understanding of how host plant abundance and distribution may affect grazing levels and herbivore feeding behaviour. A comparison of herbivory measurements between Australia and the neotropics, using the same methods, will confirm whether the continents do indeed have different grazing intensities. Lastly, long-term research on the factors (such as herbivory) affecting tree growth and regeneration may lead to more effective ecological management of disturbed rainforest regions.