

Leaf growth dynamics and herbivory in five species of Australian rain-forest canopy trees

MARGARET D. LOWMAN*

Department of Biology, Williams College, Williamstown, MA 01267, USA

Summary

1. The leaf growth dynamics of five species of rain-forest tree in New South Wales, Australia, were studied over the lifespan of several cohorts of leaves (ranging in longevity from 6 months to over 10 years), to determine the patterns of emergence, growth, mortality and herbivory in the canopy. Leaf population dynamics were examined for variability within and between several spatial scales: canopy heights, individual trees, species, and rain-forest formations.

2. Representative species were selected within each of the three major rain-forest formations of New South Wales: *Nothofagus moorei* and *Doryphora sassafras* in cool-temperate or montane or mossy microphyll forest, *D. sassafras* and *Ceratopetalum apetalum* in warm-temperate or simple notophyll vine forest, and *Dendrocnide excelsa*, *D. sassafras* and *Toona australis* in subtropical or complex notophyll vine forest. Technical climbing apparatus was used to gain access to the canopy, where leaves were permanently marked and monitored on a monthly basis for up to 12 years.

3. Three main leafing patterns were observed: seasonal growth — leaves flushed synchronously (e.g. *N. moorei*, *T. australis*); intermittent growth — leaves flushed over several months (e.g. *D. sassafras*, *C. apetalum*); and continuous growth — leaves flushed throughout the year (e.g. *D. excelsa*).

4. Leaf lifespans were variable, ranging from short-lived leaves (*D. excelsa*, approximately 6 months), to annual leaves (*T. australis*), and longer-lived leaves (e.g. *D. sassafras*, ranging from 2 to 12 or more years). Shaded leaves lived longer than sun-exposed leaves, and those on trees at montane sites generally lived longer than leaves on individuals of the same species at lower altitudes.

5. Significantly different proportions of leaf area were lost throughout the lifespan of a leaf in various species: *T. australis* (4.5%); *D. sassafras* (16.6%); *C. apetalum* (22%); *N. moorei* (31%); and *D. excelsa* (32.5%). Shade leaves and young leaves were more extensively grazed than sun leaves and old leaves, respectively. Leaves located nearer to ground level suffered greater herbivory, although this may be in part an interaction with light regime.

6. The measurements on herbivory, senescence, and longevity were used to calculate annual turnover of canopy material to either primary decomposers (through leaf fall), or primary consumers (through herbivory) in the three rain-forest formations. In a hectare of the subtropical forest, approximately 1.76 t (14%) and 5.59 t (46%) were allocated each year to herbivores and decomposers, respectively, from a total canopy of 12.26 t. In the warm-temperate forest, 2.5 t (22%) and 4.05 t (35%) were allocated annually to herbivores and decomposers, respectively, from a canopy of 11.41 t. In the cool-temperate forest, an estimated 2.63 t (27%) and 3.53 t (37%) went to herbivores and decomposers, respectively, from a total canopy of 9.69 t.

Key-words: canopy ecology, canopy turnover, leaf grazing, leaf longevity, phenology

Journal of Ecology 1992, **80**, 433–447

Introduction

Leaf growth patterns have been well documented in northern temperate hardwood forests where deciduous trees exhibit predictable annual losses of their entire canopies and subsequent, homogeneous replacement the following spring (e.g. Bormann & Likens 1979; Kikuzawa 1983). Deciduous leafing patterns have been quantified with respect to species (e.g. Sharik & Barnes 1976), sites (e.g. Leith 1974) and many environmental factors (Larcher 1975). Patterns of leaf growth in rain forests have not been well documented (but see Medway 1972; Frankie, Baker & Opler 1974; Leigh & Windsor 1982). In many tropical and subtropical rain forests, including those of Australia, even a general phenology of the canopy has not been described. Most rain-forest trees are evergreen, with lower canopies often as high as 20–30 m, making observations of leaves logistically difficult. No quantified studies of any aspects of canopy ecology for Australian rain-forest trees have been published.

Whitmore (1984) defined four types of leafing periodicity in the Asian tropics: evergrowing, manifold (different limbs at different stages), intermittent (periodic major flushes although still evergreen), and deciduous. Other terminologies include summergreen, ephemerals, wintergreen, and evergreen species (Bell & Bliss 1977); or succeeding type, intermediate type and flush type (Kikuzawa 1983). In the neotropics, most information on the phenology of canopy leaves has been published as casual information in relation to herbivory (e.g. Coley 1982), population dynamics of animals (e.g. Wolda 1982), or nutrient cycling and litterfall (e.g. Wiegert 1970; Ewel 1976); this applies also to rain forests in Africa (e.g. Hladik 1978), New Guinea (e.g. Wint 1983) and Australia (e.g. Selman & Lowman 1983).

Rain-forest leaf lifespans are usually generalized as several years (e.g. Richards 1952), although records of up to 25 years are reported (e.g. *Araucaria*; Molisch 1928). Reich *et al.* (1991) listed a range of leaf lifespans in Amazonian trees from 1.5 months to over 5 years. Leaf lifespans are regulated by consumption (herbivores or pathogens), mechanical damage (e.g. hail, wind), physical factors (e.g. water deficit), or genetically determined natural senescence (Chabot & Hicks 1982). Herbivory is the most commonly measured aspect of leaf dynamics, and rain-forest estimates usually range from 3% to 10% of leaf surface area (e.g. Odum & Ruíz-Reyes 1970; Benedict 1976), although most studies are conducted over short durations (<1 year). However, when insect grazing has been monitored over longer periods (>1 year) (Lowman 1984), higher herbivory (20–25%) has been reported (Coley 1983; Lowman 1985), and some long-term studies of several species record high variability of herbivory (Lowman 1985; Brown & Ewel 1987, 1988). Reported cases of insect

outbreaks in tropical tree canopies are rare (Wong *et al.* 1990), although this may reflect the logistic difficulties of making such observations. *Dendrocnide excelsa* has periodic infestations by a chrysomelid beetle (Petrie 1906; Lowman 1982a), the only report for an Australian rain-forest tree. Other than these isolated events, herbivory has historically been considered an insignificant event in forests (Hairston, Smith & Slobodkin 1960; Landsberg & Ohmart 1990). Mechanical damage by wind has also been recorded to affect leaf longevity, but as an infrequent event (Webb, Tracey & Williams 1972; Olsen 1990).

The rain-forest canopy is very different from the understorey layers in physical environment, biomass distribution and species composition (Elton 1973; Perry 1978; Lowman 1985). Few studies have been conducted in the upper canopy, however, despite the fact that it is the largest component of the forest both spatially and in terms of productivity. This apparent neglect probably reflects the logistical problems of access. Fortunately, the recent development of technical climbing apparatus (Perry 1978) has facilitated vertical ascent into treetops. Canopy research has been summarized by Mitchell (1982), and is expanding (e.g. Nadkarni 1984; Lowman 1985), but many questions remain unanswered.

In this study, cohorts of leaves in a rain forest were examined for growth, survivorship and mortality to answer the following questions:

1. What factors affect the patterns of leaf growth dynamics within and between Australian rain-forest trees?
2. What are the rates of turnover of leaf material to herbivores and decomposers?
3. How do grazing and leaf-fall patterns vary on spatial and temporal scales?
4. How much leaf material exists in a mature rain-forest canopy at any one time?

Methods

STUDY SITES AND SPECIES

At least two representative sites of each of the three major rain forests in New South Wales were selected for field work. The replication of sites facilitated comparisons of tree species both within and between rain forests. The sites included: subtropical or complex notophyll vine forest at Dorrigo National Park (30°20'S, 153°E, 800 m a.s.l.) and Mt Kcira Reserve (34°30'S, 151°30'E, 400 m a.s.l.); and warm-temperate or simple notophyll vine forest at Dorrigo and Royal National Parks (34°10'S, 151°30'E, 60 m a.s.l.); and cool-temperate or mossy microphyll forest at two sites in New England National Park (30°30'S, 152°E, 1400 m a.s.l.) (Fig. 1). More-extensive site information is listed elsewhere (Lowman 1982a, 1986). Sites were restricted

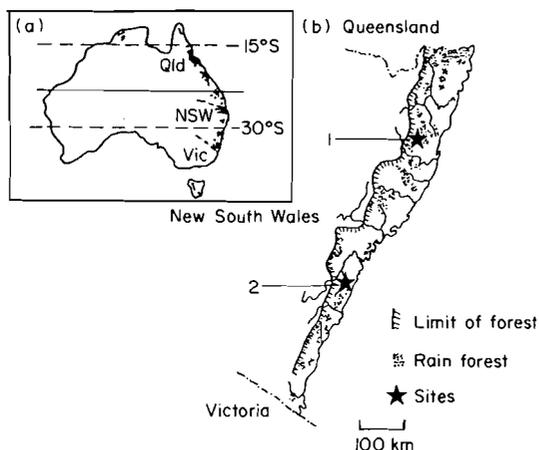


Fig. 1. Location of study sites in eastern Australia. (a) Distribution of rain forests discontinuously along the east coast; (b) map of New South Wales coast with (1) northern sites (New England National Park with cool-temperate rain forest, and Dorrigo National Park with both subtropical and warm-temperate rain forests) and (2) southern sites (Royal National Park with warm-temperate and Mt Keira Reserve with subtropical rain forests).

to national parks, because there was an active rain-forest logging policy in most regions of Australia at the time of this study (1979–90).

Five species were chosen for field measurements, because it was not logistically feasible to examine all canopy species throughout each site. The species were selected on the following criteria: commonness in one of the rain-forest types (subtropical, warm- or cool-temperate); morphological characteristics of particular interest to leaf survival, especially in relation to herbivory (e.g. presence of hairs or heavy cuticle); and apparent variability of growth patterns (e.g. deciduous vs. evergreen). Further information on the frequency of species at each site, and canopy structure is listed by Lowman (1982a, Table 5.11; 1986). The species selected were as follows:

Ceratopetalum apetalum D. Don (coachwood) (Cunoniaceae)

A common canopy tree in the warm-temperate forest. Of the two study sites, Royal National Park is near the southern limit of its range, and Dorrigo National Park is in the centre of its distribution.

Doryphora sassafras Endl. (sassafras) (Monimiaceae)

A canopy tree in two formations: subtropical (Dorrigo National Park and Mt Keira Reserve) and warm-temperate forests (Dorrigo and Royal National Parks), and an understorey tree in the cool-temperate forest (New England National Park). It grows in the widest range of habitats of the five species studied.

Dendrocnide excelsa (Wedd.) Chew (stinging tree) (Urticaceae)

Occurs in subtropical forests (Dorrigo National Park and Mt Keira Reserve). Its fast opportunistic growth enables it to colonize small treefall gaps and

cleared areas. In addition to fast regeneration, it also persists as a canopy emergent in subtropical stands, growing to 40 m. It has numerous stinging hairs covering the leaf blades and petiolar surfaces of stinging trees suggesting the evolution of morphological plant defences against predators (Petrie 1906). It also has soft mesomorphic leaves, which suggests that it may have more rapid, continuous turnover of leaves than other Australian rain-forest species.

Nothofagus moorei F. Muell. (antarctic beech) (Fagaceae)

Distributed in cool-temperate forest, usually above 600 m in NSW (New England National Park for this study) where it forms single-species stands in these moist, montane sites (Connell & Lowman 1989). This tendency to form single-species stands lends particular interest to the beech–herbivore interactions as compared to other more-diverse rain-forest formations: members of Fagoidae, including *Nothofagus*, are renowned for high leaf toughness and toxicity (Lowman & Box 1983).

Toona australis (F. Muell) Harms (red cedar) (Meliaceae)

Important in rain-forest timber history in Australia, because its red softwood was much sought by loggers. Cedar is one of the few deciduous Australian rain-forest trees. Logging has severely reduced its distribution, and the remaining individuals may not sustain the herbivore loads reported at the turn of the century (e.g. tip-moth outbreaks (Francis 1970; Floyd 1990)).

The distribution of species, according to habitats in order of increasing structural and taxonomic complexity, is: cool-temperate (*Nothofagus moorei*, *Doryphora sassafras*), warm-temperate (*Ceratopetalum apetalum*, *D. sassafras*) and subtropical (*Dendrocnide excelsa*, *D. sassafras*, *Toona australis*).

MEASUREMENTS OF LEAF GROWTH DYNAMICS

Leaf growth was measured monthly for 5 years (1979–83), during which time over 99% of the marked leaves (4183 in total) completed their life cycles. A few leaves (<20) were longer-lived and subsequently monitored for over 12 years. Leaf cohorts were marked in the canopy in different light regimes, heights, species, individual trees, and sites. Isolated events in the life of a leaf were quantified, including date of emergence, length of survival, proportion of leaf-area losses to herbivores, date of senescence, and rate of decay. The extent of replication of leaves was determined by pilot studies using leaf size to indicate environmentally different regions in the canopy (Lowman 1985). For example, because *C. apetalum* leaves varied significantly in

size with respect to light levels, canopy heights, individual trees, and sites, leaves within each of these categories were monitored. In contrast, *D. excelsa* had a homogeneous canopy, so all leaves within each tree were pooled as one population.

Leaf cohorts consisted of at least three shoots in each region of canopy monitored. Depending upon the heterogeneity of canopy as defined in the pilot study, between 200 and 1000 leaves were measured for each species. Leaves were marked during autumn 1979 (March–April), and checked monthly until senescence. Leaves were numbered sequentially from the base of the shoot upwards, each shoot consisting of 8–15 leaves. Black waterproof pens were used to inscribe small numbers on the adaxial surface. The ink was not considered to affect sampling, because a pilot study showed that it did not significantly attract or deter herbivores (Lowman 1982a). New leaves were marked and monitored as they emerged, although no new leaves were added to the survey after 3 years. Results of leaf emergence, monthly herbivory levels, and senescence were calculated from the first 3 years of data only, because the sample size were greatest then. Subsequent observations of the remaining leaves after 1983 were made only to quantify longevity and to compare young- vs. old-leaf herbivory.

Leaves were measured at three heights: ground level (<5 m), mid-canopy (5–10 m), and upper canopy (>10 m), and two light levels (sun, shade). Climbing techniques and ropes were used to gain access to most tree canopies (Perry 1978). Ladders were used for access to *N. moorei* canopies because its branches were often rotten. Adjacent trees were climbed to reach *D. excelsa* because its foliage was hazardous (due to the stinging hairs) and its wood was very weak.

Four major variables in the life cycle of a leaf were monitored: leaf emergence, leaf longevity, herbivory, and leaf fall. A fifth event, leaf decay, is reported elsewhere (Lowman 1988). Analyses of variance were performed on many of the data sets, because the experimental design was set up to compare spatial and temporal variables between different groups of leaves. Where necessary, homogeneity of variance was achieved by $\log(x + 1)$ transformation before the analyses. Student–Neuman–Keuls tests were used to rank significant results (Snedecor & Cochran 1967).

LEAF EMERGENCE

Patterns of leafing were determined by plotting monthly leaf emergence as a proportion of the total number of leaves that emerged on a given number of shoots from 1979 to 1983. Data were expressed on a percentage basis rather than by actual numbers of leaves emerging, because different species and shoots varied in actual numbers of leaves emerging.

(For example, up to 15 leaflets bud^{-1} emerged in October on *T. australis*, quite different from a shaded *C. apetalum* shoot where only 2 leaves emerged; but both may represent 75% of annual leafing.) The phenology of flowering and fruiting for each tree and its neighbours was also observed (Lowman 1982a).

LEAF LONGEVITY

The average lifespan of leaves in the canopy was estimated by calculating the number of months between emergence and abscission for all marked leaves. Only leaves reaching 'mature' status (termed 'age class 3', Lowman & Box 1983) were used to calculate longevity, because they comprised the major photosynthetically active portion of the canopy. Leaves that died during expansion phases were not included in longevity calculations, because that would underestimate the mean lifespan of the surviving canopy. Leaves were grouped into monthly cohorts (flushes) and survivorship curves were constructed.

HERBIVORY

Proportions of leaf surface area missing were measured monthly for the duration of a leaf's lifespan using a Lambda Area Meter (model 3000) and leaf tracings (Lowman 1984). In cases where losses were obvious (e.g. halves of leaves, or one pinhole), the percentage estimates (e.g. 50%, 1%) were by eye. Amounts grazed were recorded at the end of each month, as well as annually and cumulatively for the duration of leaf life. Leaf damage due to miners, galls or other types of herbivores were also recorded. Monthly data were averaged for three years (1979–82) when the sample sizes were greatest. By 1982, the majority of original marked leaves had senesced, although a small proportion lasted much longer.

Complete defoliation was distinguished from natural senescence by observation: older leaves that remained intact for several years and suddenly disappeared were recorded as senesced; younger leaves that showed signs of damage (e.g. insect frass or herbivores feeding) and progressively diminished leaf area during periods of insect activity (Lowman 1982b) were recorded as eaten. It is conceivable that some events recorded as leaf fall were actually herbivory by insects whose feeding was extremely rapid or patchy (e.g. stem borers), and thereby not accounted for in monthly measurements. The results therefore reflect only directly observed grazing activities, and may slightly underestimate the amounts of leaf material consumed. Herbivory data were expressed by proportion (%) leaf area missing, but were transformed to increments (cm^2) eaten by measuring average leaf sizes (Lowman 1987).

LEAF FALL AND TURNOVER

Leaf fall was measured in 1-m × 1-m traps, with at least 12 traps situated throughout each site. Leaf decay rates were reported elsewhere (Lowman 1988).

Estimates of monthly changes in biomass of leaf material were calculated for the three rain-forest formations. I extrapolated average monthly litterfall weights to $\text{t ha}^{-1} \text{ year}^{-1}$ (called 'actual leaf biomass') and added the measured amounts of leaf surface area defoliated to obtain 'potential leaf biomass' (i.e. amount of canopy that would exist in the absence of herbivory). Information on other species (in addition to the five here) was obtained from

litterfall collections and phenological observations (Lowman 1982a), and was used to calculate proportions of each species in the forest canopy to make accurate extrapolations.

Results

LEAF EMERGENCE

Dendrocnide excelsa exhibited a continuous leafing pattern (albeit with a summer peak); leaves emerged during 11 months of the year (Fig. 2a). Winter (May–August) marked the period of lowest leafing activity, which was also when flowering and fruiting

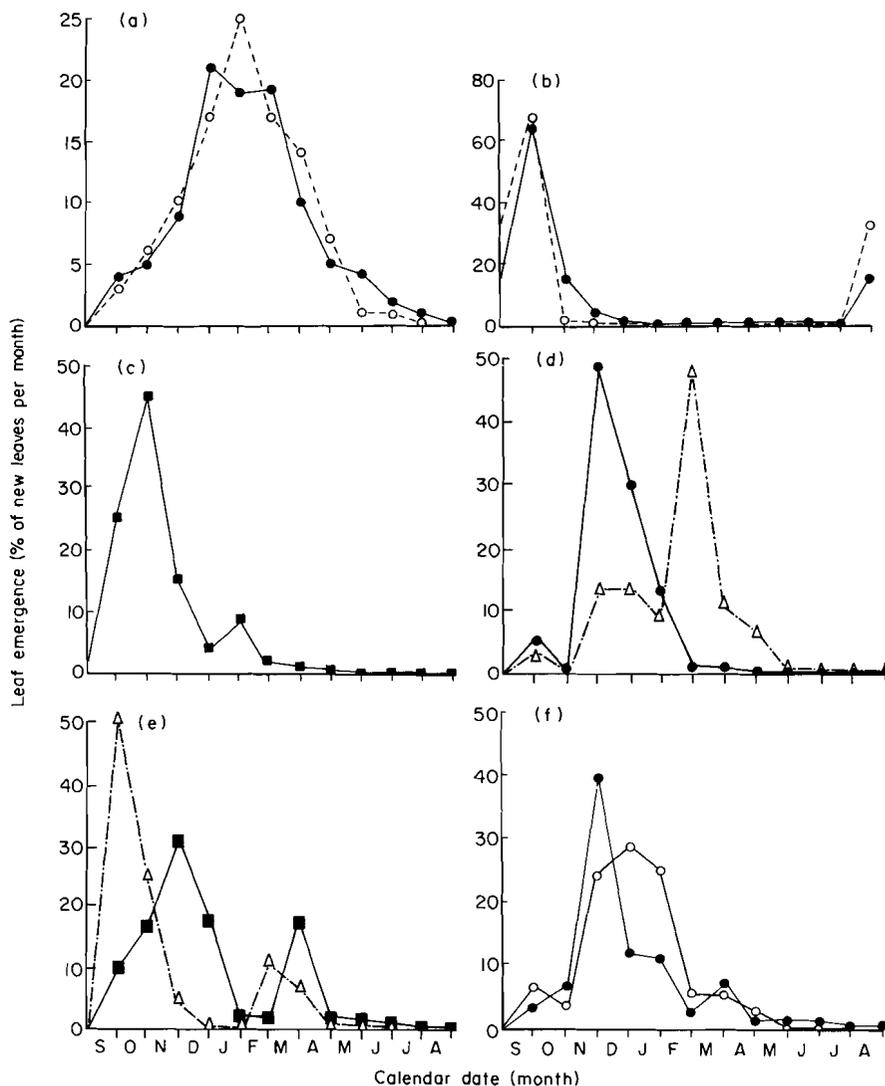


Fig. 2. Leaf emergence of five rain-forest canopy tree species in New South Wales. Shapes of symbols are matched with rain-forest type: cool-temperate (\square , \blacksquare), warm-temperate (\triangle , \blacktriangle) or subtropical (\circ , \bullet). In case where leaves were compared between light levels, sun and shade leaves are represented by light and dark symbols, respectively. (a) *Dendrocnide excelsa* and (b) *Toona australis* in two subtropical rain-forest sites at Mt Keira (\circ) and Dorrigo National Park (\bullet); (c) *Nothofagus moorei* in the cool-temperate rain forest at New England National Park (\blacksquare); (d) *Ceratopetalum apetalum* in warm-temperate rain forest at Royal National Park (\triangle) and subtropical rain forest at Dorrigo National Park (\bullet); (e) *Doryphora sassafras* in cool-temperate rain forest (\blacksquare) at New England National Park and warm-temperate rain forest (\triangle) at Royal National Park; (f) *D. sassafras*, illustrating differences between sun (\circ) and shade (\bullet) portions of the canopy in a subtropical site at Dorrigo National Park. Points indicate percentage of new leaves emerged for each month, averaged over 1979–83.

occurred. Leafing patterns were nearly identical at the two sites, with negligible annual variation.

Nothofagus moorei, although not deciduous, also exhibited a spring flush, but only half the canopy leafed each year, and the other half remained green until the following autumn (Fig. 2c). In cases of severe defoliation (Selman & Lowman 1983), *N. moorei* canopies underwent a smaller leaf flush in mid-summer (January).

Deciduousness was rare in the Australian rain-forests, and only one species (*Toona australis*) exhibited this habit, with its accompanying simultaneous leaf flush in early spring (September–October) (Fig. 2b). The most common pattern was intermittent flushing, with leaf flushes occurring from spring until autumn (September–April), albeit

with summer peaks (e.g. *Ceratopetalum apetalum* (Fig. 2d) and *Doryphora sassafras* (Fig. 2e,f). Shade leaves flushed several weeks earlier than sun leaves within the subtropical canopy (Fig. 2f). Budburst was observed to be 1 or 2 weeks earlier at higher than at lower canopy levels, but this time lag was not obvious from monthly data. Most rain-forest canopy tree species exhibited intermittent leafing (Lowman 1982a).

LEAF SURVIVAL

Dendrocnide excelsa leaves were relatively short-lived, with a longevity of approximately 7 months that was statistically similar between the two sites sampled ($F_{1,58} = 0.66$, NS) (Table 1). A survivorship

Table 1. Mean (\pm SE) leaf longevity and herbivory (the percentage (\pm SE) of leaf area eaten) of different cohorts of leaves of five species of rain-forest canopy trees in New South Wales

Rain-forest type and location	Leaf lifespan (months)	Number of leaves measured	Herbivory (%)
<i>Dendrocnide excelsa</i>			
Subtropical			
Dorrigo	6.7 \pm 0.40	146	32.5 \pm 2.6
Mt Keira	7.2 \pm 0.70	95	15.5 \pm 1.4
Average annual canopy loss (%)		242	42.0
<i>Toona australis</i>			
Subtropical			
Dorrigo	9.5 \pm 0.22	99	6.3 \pm 0.3
Mt Keira	7.4 \pm 0.14	275	3.3 \pm 0.2
Average annual canopy loss (%)		374	4.5
<i>Nothofagus moorei</i>			
Cool temperate			
New England	22.9 \pm 0.21	1967	31
<i>Ceratopetalum apetalum</i>			
Warm-temperate			
Royal	43.0 \pm 3.2	395	21.3
sun only	24.9 \pm 1.1	245	26.9 \pm 2.0
shade only	60.1 \pm 2.7	150	35.3 \pm 2.5
Dorrigo	58.0 \pm 4.3	190	24.0
sun only	26.9 \pm 1.8	110	9.4 \pm 1.1
shade only	88.6 \pm 4.4	80	35.3 \pm 2.7
Average annual canopy loss (%)		585	22.0
<i>Doryphora sassafras</i>			
Subtropical			
Dorrigo	41.3 \pm 1.7	694	15.0
sun only	22.5 \pm 1.1	390	13.4 \pm 2.0
shade only	60.0 \pm 1.4	304	16.3 \pm 2.2
Warm-temperate			
Royal	50.0 \pm 1.9	151	22.7
sun only	24.0 \pm 1.1	81	17.6 \pm 2.2
shade only	76.5 \pm 1.3*	70	27.8 \pm 2.6
Cool-temperate			
New England	53.8 \pm 1.7	170	13.6 \pm 2.0
Average annual canopy loss (%)		1015	16.6

* Slightly higher, because six leaves of the sample size of 1015 leaves were still on the tree after 12 years.

curve of the continuous leafing pattern of *D. excelsa* illustrates the overlap of leaf cohorts, creating a mosaic of leaf ages in a canopy (Fig. 3a). The leaves that emerged during winter months senesced slightly earlier than leaves that flushed during summer months. Shoots put out an average of 8.3 leaves annually.

In contrast, *Toona australis*, with its deciduous canopy and synchronous spring leafing, had a simpler distribution of leaf cohorts in the canopy at one time (Fig. 3b). Average leaf longevity was <1 year, and was significantly longer at Dorrigo National Park (the northern site) than at Mt Keira (the southern site) ($F_{1,98} = 14.08$, $P < 0.001$).

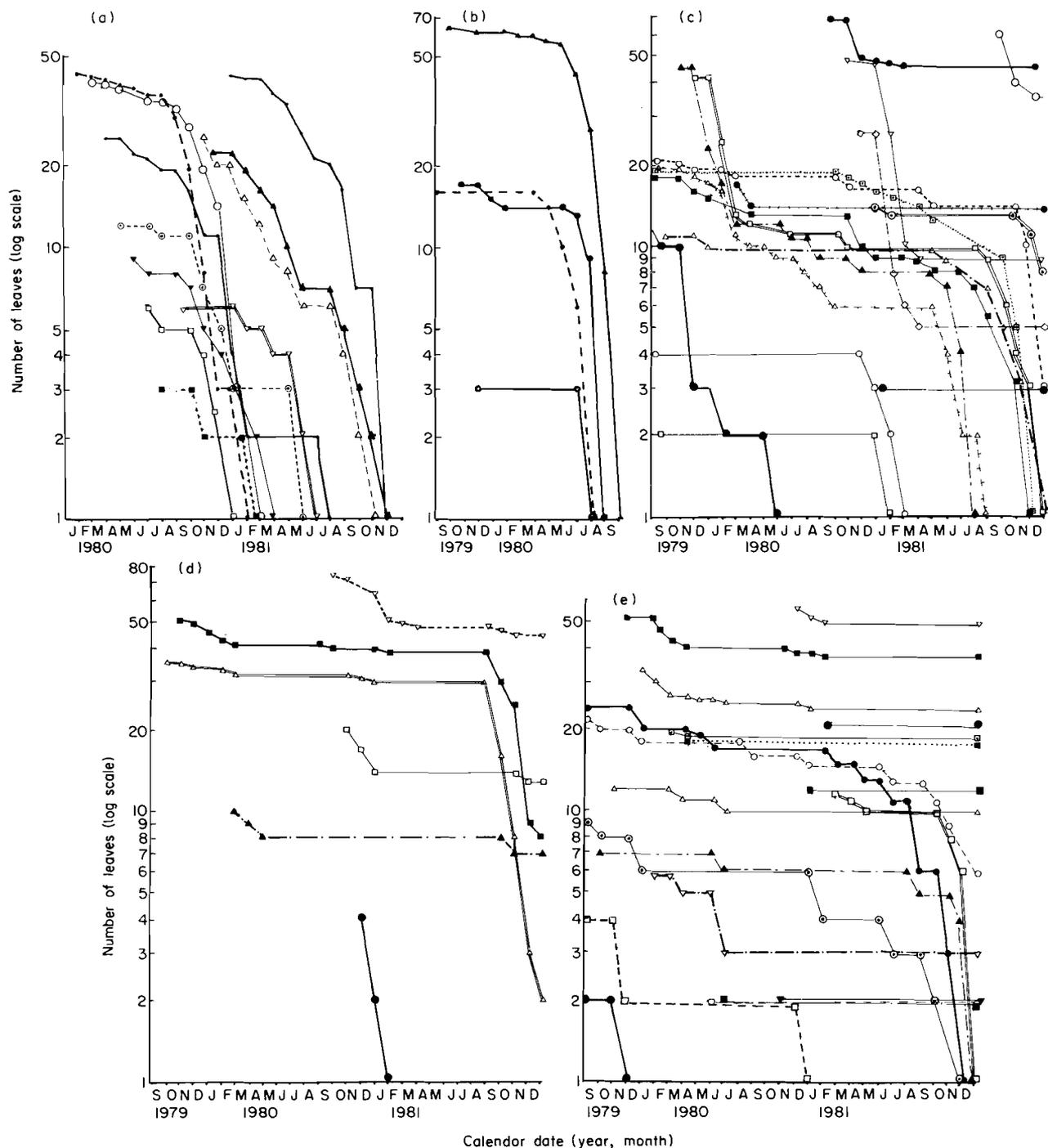


Fig. 3. Leaf survivorship curves for five rain-forest canopy tree species in New South Wales. (a) *Dendrocnide excelsa* with continuous leafing and short-lived leaves; (b) *Toona australis* with synchronous leafing and a deciduous habit; (c) *Nothofagus moorei* with a bimodal leafing pattern and evergreen leaves; (d) *Ceratopetalum apetalum* with intermittent leafing and evergreen leaves; (e) *Doryphora sassafras* with intermittent leafing and evergreen leaves. For each species, survivorship data are presented for the first 12 months of leaf-flush activity following commencement of study (plus the leaf cohorts already present on the branches) and graphed until >50% of those leaves had fallen. Leaves were included from nine shoots representing three shoots from each of three trees (except for *N. moorei* and *C. apetalum* which had 18).

The other three species observed were evergreen and intermittent in their leafing patterns, thereby creating a complex mosaic of leaf age classes and distributions throughout tree canopies. Even *Nothofagus moorei*, which had leaves that were relatively short-lived (22.9 months) (Table 1), had canopies that were composed of at least six different cohorts of leaves at one time (Fig. 3c). During their first weeks, the leaves were extremely prone to insect attack; but if they survived this critical period, their lifespan usually extended to nearly 2 years. Juvenile leaf-mortality was >50% for spring flushes (when herbivores were most abundant) (Selman & Lowman 1983). Leaf survivorship patterns for *Ceratopetalum apetalum* (Fig. 3d) and *Doryphora sassafras* (Fig. 3e) show evergreen canopies with relatively long-lived leaves.

Most canopy trees in the subtropical and warm-temperate had leaves with similar physical attributes: highly sclerophyllous, elliptical in shape, with drip tips, serrations or intermittent teeth, and evergreen. Their phenology and herbivory had similar patterns, which are exemplified by both *C. apetalum* and *D. sassafras*. They suffered high juvenile mortality from insect herbivores, and those that escaped defoliation usually survived a normal lifespan of approximately 2 years (sun leaves) to 6 years (shade leaves) with some *D. sassafras* leaves still intact after 12 years (Table 1). If a cohort of leaves escaped juvenile mortality by insect defoliation, abscission occurred gradually over several years.

HERBIVORY

Herbivory patterns varied between species (Fig. 4), but peaks in leaf consumption occurred just after leaves emerged (Fig. 2). The continuous-leafing species, *Dendrocnide excelsa*, suffered herbivory throughout the year (Fig. 4a), although defoliation was highest during summer (5% per month during November–February) which was also its peak time of leafing. Variability in herbivory between months was significant ($F_{11,12} = 3.79$, $P < 0.05$) but was highest in January. Average leaf area loss over the lifespan of a leaf was 32.5% (or 88.8 cm² of leaf surface area) in Dorriggo and 15.5% (or 42.5 cm²) in Mt Keira, based on mean leaf size of 273.12 cm². But, because most individual leaves lived for <1 year, the annual canopy loss for individual trees was as high as 42% of its annual leaf production. The stinging hairs, which may provide effective chemical defence against mammalian predators in Asia (Chew 1969), appear less successful against the host-specific chrysomelid beetle *Hoplostines viridipennis* in Australia. Other herbivores are listed elsewhere (Lowman 1985).

Herbivory of *Nothofagus moorei* also varied significantly among months ($F_{11,12} = 8.93$, $P < 0.001$). Mean proportions of 8.8% and 11% were removed

in October and November, respectively, declining to 0% during winter months (Fig. 4b). Herbivory was significantly higher in young leaves than old ($F_{1,98} = 1384.3$, $P < 0.001$); leaves lost approximately 54% of their surface area during their first year and only 0.22% in their second year, averaging 31% annually (weighted according to the proportion of leaves that survived to their second year). Coleoptera were the major herbivores in beech canopies, and the larvae of *Novocastria nothofagi* Selman severely defoliated new flushes during spring (September–October) (Selman & Lowman 1983). As for all species studied, physical tearing played a negligible role in beech leaf mortality (as compared to herbivory), with <1% lost during windy conditions. Desiccation occasionally occurred in partially eaten young leaves, although this was also rare.

The evergreen canopies of *Ceratopetalum apetalum* averaged 22% annual leaf-area loss, with statistically similar amounts of 21.3% and 24% between two warm-temperate sites at Royal and Dorriggo National Parks, respectively ($F_{1,98} = 0.26$, NS) (Table 1, Fig. 4c). The highest defoliation occurred at the time of leaf emergence (October–December; Fig. 4c,d), with a second, smaller flush in late summer (February–March). Herbivory was higher in the shade than in the sun: 35.3% vs. 9.4% at Dorriggo annually ($F_{1,98} = 28.31$, $P < 0.001$) (Fig. 4d). Shade herbivory showed a bimodal temporal pattern, while sun-leaf herbivory peaked in November. Herbivory also varied between canopy heights, with significantly lower defoliation at levels >10 m, as compared to middle (5–10 m) or low (<5 m) canopy levels ($F_{2,72} = 4.13$, $P < 0.05$).

Toona australis suffered the lowest herbivory levels of any species measured, averaging 4.5% annual loss (Table 1). Defoliation was significantly different between months, with the highest removal of 2.25% during November in the subtropical forest (Fig. 4e). (This amount comprised less than that half the average monthly loss for *D. excelsa*.) A characteristic gall (agent unknown) infested approximately 25% of the *T. australis* leaflets in both sites, but did not cause premature senescence.

Annual leaf area losses for *D. sassafras* averaged 16.6% and were similar between sites ($F_{2,117} = 0.55$, NS) and between individual tree ($F_{3,76} = 0.17$, NS). Herbivory patterns exhibited one summer peak in the subtropical forest (Fig. 4h), but were bimodal in the warm and cool-temperate forests (Fig. 4f,g). Shade leaves had higher defoliation than sun leaves, 16.3% vs. 13.4% ($F_{1,58} = 5.89$, $P < 0.05$). This is discussed elsewhere in relation to toughness and leaf chemistry (Lowman & Box 1983). Shade leaves at a height of 1 m had higher defoliation than shade leaves at 5 m or 15 m (39%, 21.3% and 13%, respectively).

In all five species, the herbivores observed feeding in canopies were predominantly Coleoptera: Cur-

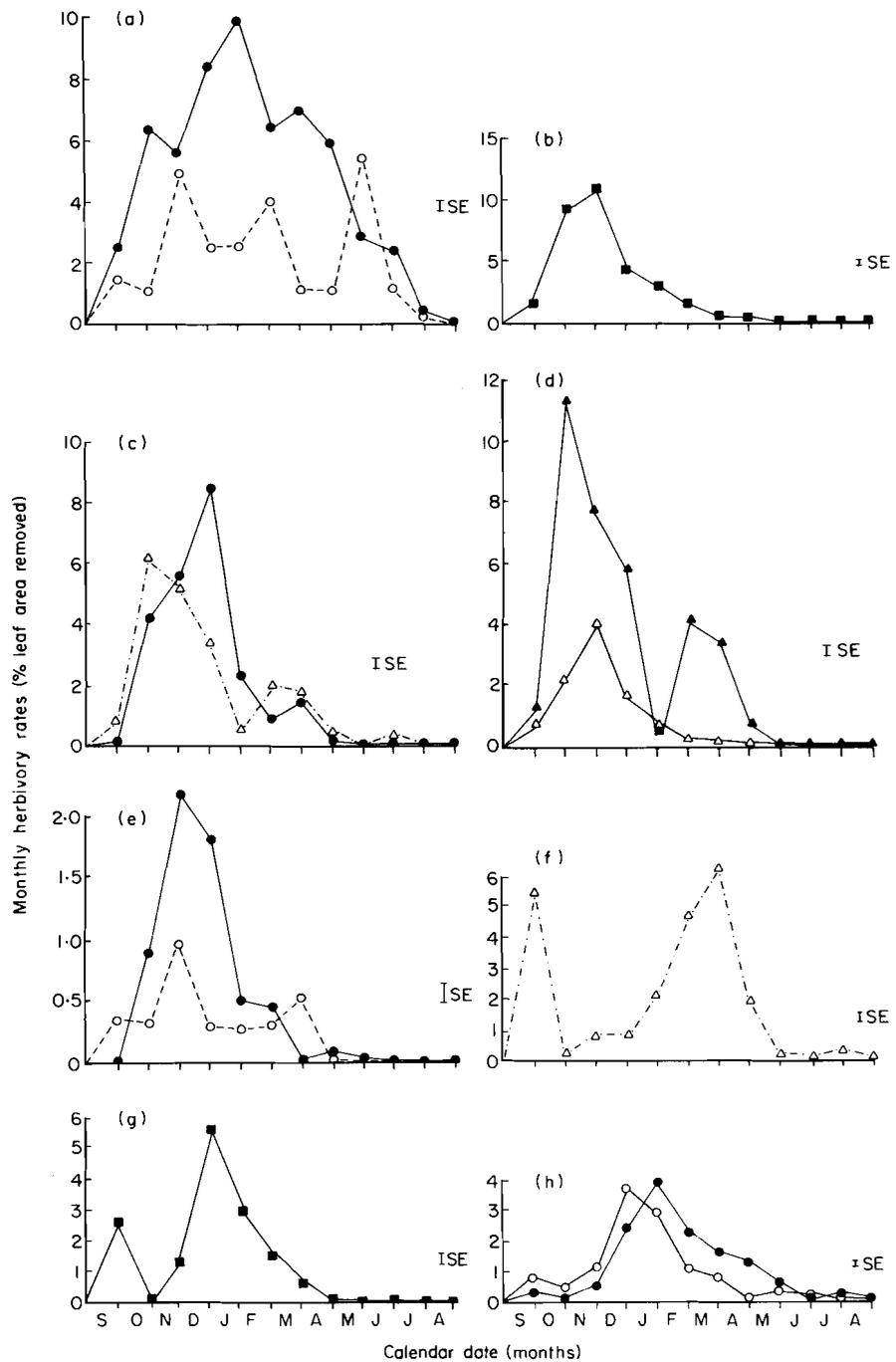


Fig. 4. Herbivory of five rain-forest canopy tree species in New South Wales: (a) *Dendrocnide excelsa* at two subtropical sites, at Mt Keira (○) and Dorrigo National Park (●); (b) *Nothofagus moorei* in the cool-temperate rain forest at New England National Park (■); (c) *Ceratopetalum apetalum* in subtropical (Dorrigo National Park) (●) and warm-temperate (Royal National Park) (△) forests; (d) *Ceratopetalum apetalum* in sun (△) and shade (▲) portions of a warm-temperate canopy at Royal National Park; (e) *Toona australis* in two subtropical sites (symbols as for (a)); (f) *Doryphora sassafras* in warm-temperate canopy (Royal National Park); (g) *D. sassafras* in a cool-temperate forest (New England National Park); (h) *D. sassafras* in sun (○) and shade (●) portions of a subtropical canopy (Dorrigo National Park). Points indicate percentage of leaf surface area that was eaten each month, averaged over 1979–83.

culionidae (Lowman 1985). Most species appeared polyphagous, usually feeding on canopy leaves of neighbouring species. For example, beetles observed feeding on *D. sassafras* were also on adjacent canopies of *C. apetalum*, *Schizomeria*

ovata D. Don and *Sloanea australis* (Benth.) F. Muell. One weevil, *Apion* sp., was particularly common on *D. sassafras*, with up to 10 on leaves of both upper and lower canopies from Mt Keira in NSW to Lamington National Park in Queensland.

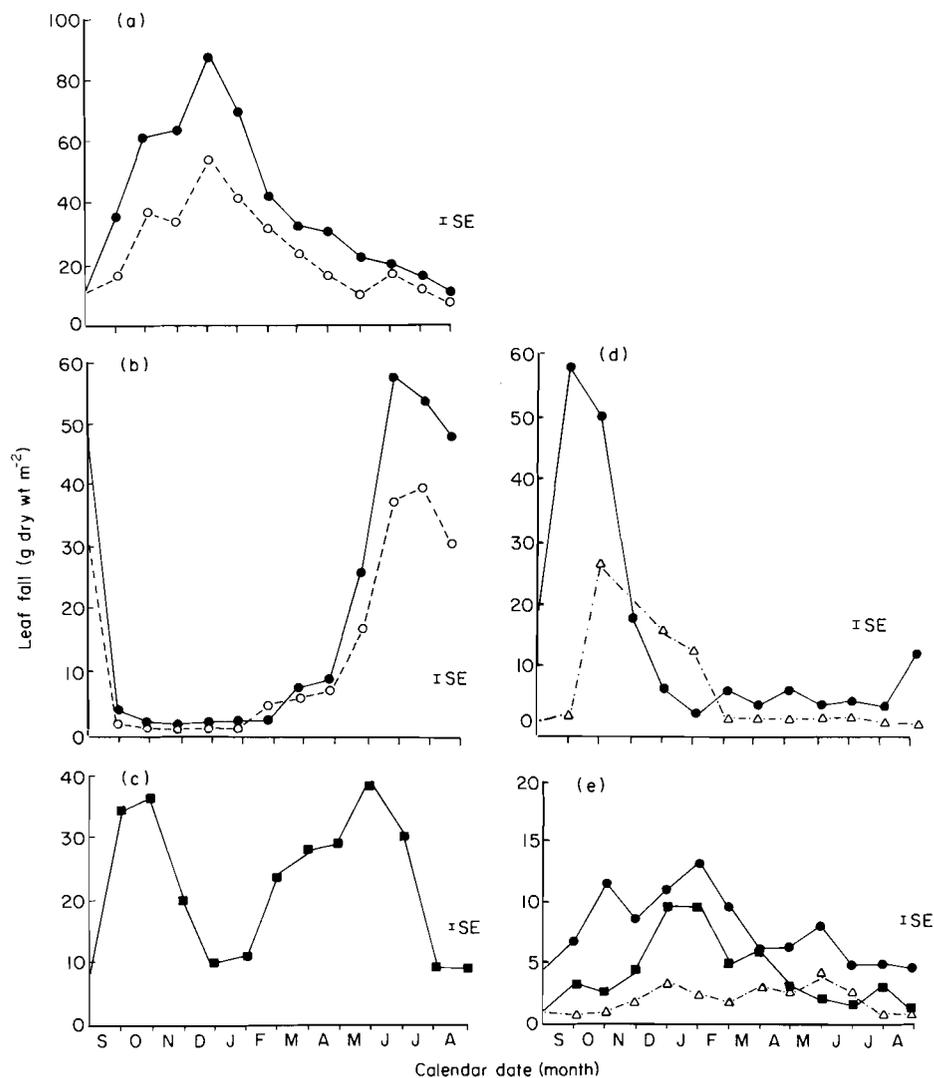


Fig. 5. Leaf fall of five rain-forest canopy tree species in New South Wales: (a) *Dendrocnide excelsa* and (b) *Toona australis* in two subtropical sites, at Mt Keira (○) and at Dorrigo National Park (●); (c) *Nothofagus moorei* in the cool-temperate rain forest at New England National Park (■); (d) *Ceratopetalum apetalum* in subtropical rain forest (●) at Dorrigo National Park and warm-temperate rain forest (△) at Royal National Park; and (e) *Doryphora sassafras*, the only species found in all three rain-forest formations (symbols for sites as above). Points indicate mass of leaf material (g dry wt m^{-2}) falling each month, averaged over 1979–83.

LEAF FALL AND TURNOVER

Leaf fall of *D. excelsa* peaked during summer (December–January) but continued throughout the year (Fig. 5a), similar to its continuous pattern of leaf emergence. This species had soft, mesomorphic leaves; consequently decay was rapid, requiring just over 4 months (Lowman 1988).

Leaf fall was a synchronous, annual event in *T. australis* that occurred at the onset of winter (June–July) (Fig. 5b). The trees were bare for only 1–2 months before leafing out again in early spring. Leaves required just over 1 year to decay fully (Lowman 1988).

Because *N. moorei* predominated in the cool-temperate forest canopy, its leafing patterns dominated the ecosystem. Leaves fell during every

month of the year, but with two peaks: in autumn (May–June) during storm winds, and in spring (October) (Fig. 5c). In total, half the canopy fell each year (leaf lifespan = 2 years). This was one of the few species in Australian rain forests which had leaves that often turned red or yellow before abscission. Leaf litter decayed slowly, with a half-life of 16 months. Leaves falling to the forest floor in summer (January) disappeared faster than leaves falling in winter (August) (Lowman 1988).

Leaf fall of *C. apetalum* occurred simultaneously with leaf emergence, so this species always retained at least half its canopy. Leaf fall peaked during spring (September–October) and was negligible during winter (Fig. 5d). The pattern of leaf decay was typical of Australian rain-forest species, with a half-life of 10.5 months (Lowman 1988).

Leaf fall of *D. sassafras* peaked during summer (December–January), with a smaller autumn peak in May (Fig. 5e). This pattern was consistent in all three rain-forest formations. *D. sassafras* leaves decayed fastest in the subtropical forest (half-life of 4.5 months), and slowest in the cool-temperate forest (half-life of 14.5 months), with an intermediate rate in the warm-temperate forest (half-life of 6.5 months) (Lowman 1988). Decay was fastest during the summer and slowest in the winter at all forests.

GENERAL RAIN-FOREST CANOPY DYNAMICS

The average production of leaf material in the three rain forests ranged from 7.06 to 10.5 t ha⁻¹ year⁻¹, based on litterfall and herbivory measurements (Table 2). The 'actual canopy' represents the standing crop of leaf material, or canopy sustained after herbivory and other events of mortality (not total leaf material produced). In contrast, the 'potential canopy' was the gross primary production of leaf material, and ranged from 9.69 to 12.26 t ha⁻¹ year⁻¹.

All leaf material produced in the canopy was eventually channelled to either primary consumers (herbivores) or primary decomposers. In this study, a range of 6–32% of the total leaf biomass of five species was consumed by herbivores, averaging 2.3 t ha⁻¹ year⁻¹ (Table 2). Because the proportions

of each species in the canopy were already known (Lowman 1986), it was possible to calculate average amounts of herbivory for each forest type. An estimated 14–27% of leaf surface area was defoliated annually, averaging 2.3 t ha⁻¹ year⁻¹. In contrast, a range of 35–46% of the leaf material entered the decay pathway, comprising an average of 4.39 t ha⁻¹ year⁻¹ (approximately twice the amount of material entering the herbivory pathway).

The leaf growth dynamics were extrapolated in conjunction with phenological observations (Lowman 1982a) to estimate the standing crop of foliage of each rain-forest formation at different times of year (Fig. 6). The periodicity of leaf phenological events varied both within and between rain-forest formations, although some generalities were evident. In all cases, young leaves emerged and underwent relatively high levels of herbivory. Leaves that escaped herbivory during juvenile stages suffered relatively little defoliation during the rest of their lifespans. Most leaves lived for 2–3 years, and so the majority of leaf standing crop was comprised of mature leaf biomass (2- or 3-year-old leaves). The canopies of all rain forests attained maximum amounts of leaf material in late spring (October–December) when new leaves had emerged but defoliation was still underway, and old leaves had not completely fallen.

Table 2. Annual canopy turnover (t ha⁻¹ year⁻¹) of leaves in the canopies of three rain forests in New South Wales. Potential canopy refers to all foliage produced by a tree (but before herbivory); actual canopy refers to foliage produced by a tree, but without portions that were removed by herbivores. The numbers in parentheses after the turnover rates due to herbivory and decay are percentages of potential canopy. 'Other species' refers to all those species for which leaf masses were measured in litterfall traps (Lowman 1986)

Rain-forest type	Canopy turnover (t ha ⁻¹ year ⁻¹)			
	Potential	Consumed by herbivores	Decomposed	Actual
Cool-temperate				
<i>Nothofagus moorei</i>	7.91	2.42 (31%)	2.74 (35%)	5.48
<i>Doryphora sassafras</i>	1.16	0.14 (12%)	0.51 (44%)	1.02
Other species	0.62	0.06 (10%)	0.28 (45%)	0.56
Total	9.69	2.63 (27%)	3.53 (36%)	7.06
Warm-temperate				
<i>Ceratopetalum apetalum</i>	2.49	0.53 (21%)	0.89 (36%)	1.96
<i>Doryphora sassafras</i>	0.71	0.16 (23%)	0.25 (35%)	0.55
Other species	8.21	1.81 (22%)	2.91 (35%)	6.40
Total	11.41	2.50 (22%)	4.05 (35%)	8.91
Subtropical				
<i>Dendrocnide excelsa</i>	0.24	0.08 (32%)	0.28	0.16
<i>Toona australis</i>	0.30	0.02 (6%)	0.28 (93%)	0.28
<i>Doryphora sassafras</i>	1.32	0.20 (15%)	0.56 (42%)	1.12
Other species	10.40	1.46 (14%)	4.47 (43%)	8.94
Total	12.26	1.76 (14%)	5.59 (46%)	10.50
Overall mean	11.12	2.30 (21%)	4.39 (39%)	8.67

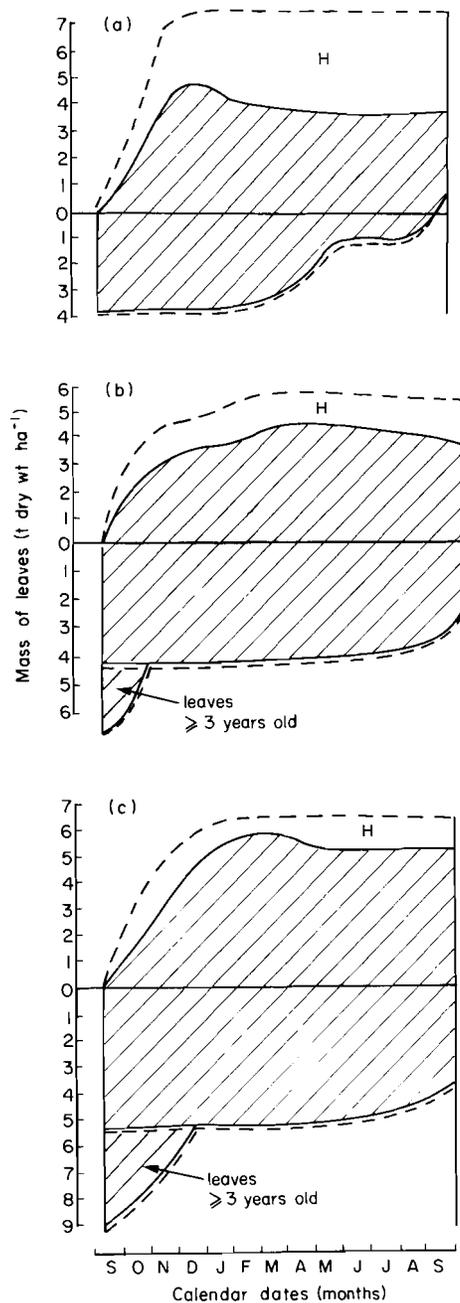


Fig. 6. Monthly fluctuations in the mass (t dry wt ha^{-1}) of leaf material in the canopies of three rain-forest formations in New South Wales: (a) cool temperate, (b) warm temperate and (c) subtropical. The hatched areas indicate the 'actual canopy' (leaf material that remains after insect herbivory), and areas outlined by dotted lines represent 'potential canopy' (leaf material produced by the trees, but before the herbivores consumed portions). Leaf growth and leaf fall are reflected in the changes of actual canopy from month to month. The areas marked by H represent the relatively large portion of new (i.e. 1-year-old leaves) eaten by herbivores. The older leaves (2 and 3 years old, or more) have almost negligible herbivory. Calculations were made by extrapolating the litterfall weights from Lowman (1988) and correcting for the leaf area eaten and leaf growth and leaf fall measured in this study.

Discussion

The high diversity within rain forest places limitations on field work. In this study, only five species were examined in great detail for leaf growth dynamics, and these may not include the entire range of canopy dynamics for a site. In the cool-temperate forest, *Nothofagus moorei* comprised over 75% of the biomass (Lowman 1986), so its leaf growth dynamics were obviously representative of the entire canopy. Even in the moderately species-diverse warm-temperate rain forest, *Doryphora sassafras* and *Ceratopetalum apetalum* accounted for almost 50% of the canopy, making the results here also representative of the entire canopy. In the subtropical forest, however, the three species studied in detail comprised only about 15% of the canopy (Lowman 1986). Furthermore, these species exhibited very different patterns of leaf growth, making it difficult to generalize about the dynamics of this community, except to recognize its variability.

Phenological records were kept for all canopy species in each site (Lowman 1982a). They confirmed that the entire cool-temperate canopy was very seasonal (as were *N. moorei* and *D. sassafras* there), that the warm-temperate canopy was moderately seasonal (as were *D. sassafras* and *C. apetalum* there), and that the subtropical rain forest had variable phenological patterns throughout the year, albeit with a major pulse in the summer. Insect abundance, particularly herbivores, followed the same pattern (Lowman 1982b).

VARIABILITY IN GROWTH PATTERNS AND HERBIVORY

Tropical and subtropical trees have evolved a range of growth patterns, not just a temperate schedule that is imposed by climate. Among the species studied, three major patterns were evident: a rapid synchronous, annual spurt of growth (e.g. *N. moorei*, *T. australis*); continuous growth (e.g. *D. excelsa*); and an intermittent pattern of continuous growth during spring and summer, alternating with a winter rest (e.g. *C. apetalum*, *D. sassafras*). These correspond to the flush type, succeeding type and intermediate type of Kikuzawa (1983), but the duration of leafing is shorter in the temperate forests he studied. Annual fluctuations of physical factors (e.g. light (Lowman (1986)) or biotic factors (e.g. insect pests (Selman & Lowman (1983))) altered the growth patterns of canopy layers or individuals on a small scale, and of entire communities on a larger scale.

Within the growth pattern observed, herbivory was critical in affecting leaf survival. Six factors were isolated that contributed to variability in

herbivory rates: leaf age, space (between branches and trees and sites), tree species, time, light regime, and sampling method (Lowman 1984). The interaction of these factors created further variability between different portions of the canopy. Of the six factors examined, leaf age caused the most striking differences: herbivores preferred young leaves over old ones, despite a proportionally greater abundance of surface area of old leaves within most canopies. If young leaves were available to herbivores over the duration of their emergence, juvenile mortality was fairly high (e.g. *N. moorei* (Selman & Lowman (1983)). In this sense, insect herbivores caused increased leaf mortality, but only to juveniles. Similarly, galls can induce leaf mortality (Williams & Whitham 1986). As leaves aged, they changed in chemical composition, with some of the longer-lived species investing more in their defences (Lowman & Box 1983; Coley 1986). Colonizing species (e.g. *D. excelsa*) tended to have shorter-lived leaves with less investment in leaf structure, and avoidance of herbivores may have been due to chance (Whitham 1981) or perhaps to seasonal avoidance (i.e. leafing out when insects were not abundant).

TURNOVER OF LEAF MATERIAL TO HERBIVORES VS. DECOMPOSERS

Both herbivory and decay represent pathways of turnover of leaf tissue. Litter fall, when taken alone, underestimates forest productivity if amounts grazed are not considered (Jordan 1971). In the present study, an average of 21% of the canopy was consumed by herbivores annually (Table 2). This loss appeared moderate, but became proportionally more significant when compared to the annual turnover of leaf material to decay. In the evergreen rain forests examined, 39% of the canopy leaves fell annually to decomposers, yet the average annual herbivory was more than half of that amount (21%).

The relative importance of the amounts of leaf material entering the herbivory pathway may become even greater when the nutrient recycling times are compared between the two pathways. Leaf decay ranged from 3 months for *D. excelsa* to 3 years for *N. moorei* with four of five species requiring over 1 year to decay (Lowman 1988). In contrast, the half-life of insect frass was approximately 6 months in Britain (millipede pellets (Nicholson, Bockock & Heal (1966)), and is presumably much faster for subtropical insects (but no comparable data are available). This raises a further question concerning the turnover of leaf material to either decay or grazing pathways: is there any energetic advantage to rapid recycling of leaf material by frass as compared to the leaf-fall pathway where decay

requires several years? Perhaps the faster recycling of leaf material grazed by insects is partial compensation for the direct loss of leaf tissue before the end of its photosynthetically active lifespan. Perhaps the slow decay of some nutrients is advantageous to species with the capability of utilizing them via mycorrhizal associations. In this study, turnover of leaf material to the decomposer pathway was greater by weight, but the amount recycled through herbivores may attain greater significance as a result of its faster return into the nutrient-cycling pathways.

The differences between leaf tissue produced by a tree (termed here 'potential canopy') and the subsequent leaf area remaining after herbivory (termed here 'actual canopy') are further complicated by many (as yet unanswered) physiological questions: how much compensatory growth does a tree undergo to sustain pest damage? how does the photosynthetically active life of a leaf alter throughout its lifespan (and how does this vary between species, or between sun and shade leaves)? and, ultimately, how much herbivory can these trees sustain repeatedly over many years? This study measured rain-forest leaf growth dynamics over a small timespan proportional to the life of a tree. No evidence of mortality of any portions of the canopies studied was observed, implying that the trees can sustain the moderately high levels of herbivory measured. Only further observations over time can substantiate this assumption.

Acknowledgments

This study was funded by a Sydney University postgraduate fellowship and the Australian Research Grants Scheme. I am indebted to Peter Myerscough, Peter Ashton, Joe Connell, Jack Schultz, Patrice Morrow, Tony Underwood and Harold Heatwole for valuable discussions over the past 12 years; and to the many students who assisted with tree-climbing, especially Margaret French, Patti Schmitt, Anna-Marie Hatcher and Wayne Higgins. Tom Weir of CSIRO kindly identified the herbivorous insects, and Geoff Tracey and Alex Floyd confirmed plant identifications when I first started fieldwork. Lynda Bridges assisted with graphics, and Sandra Higgins and John Lowman with typing and proof-reading.

References

- Bell, K.L. & Bliss, L.C. (1977) Overwintering phenology of plants in a polar semidesert. *Arctic*, **30**, 118–121.
- Benedict, F.F. (1976) *Herbivory rates and leaf properties in four forests in Puerto Rico and Florida*. PhD thesis, University of Florida, Gainesville, Fla.

- Bormann, F.H. & Likens, G.E. (1979) *Patterns and Process in a Forested Ecosystem*. Springer, Berlin.
- Brown, B.J. & Ewel, J.J. (1987) Herbivory in complex and simple tropical successional ecosystems. *Ecology*, **68**, 108–116.
- Brown, B.J. & Ewel, J.J. (1988) Responses to defoliation of species-rich and monospecific tropical plant communities. *Oecologia*, **75**, 12–19.
- Chabot, B.F. & Hicks, D.J. (1982) The ecology of leaf lifespans. *Annual Review of Ecology and Systematics*, **13**, 229–259.
- Chew, W.L. (1969) A monograph of Dendrocnide (Urticaceae). *Gardens Bulletin Singapore*, **25**, 1–104.
- Coley, P.D. (1982) Rates of herbivory on different tropical trees. *The Ecology of a Tropical Forest* (eds E.G. Leigh, A.S. Rand & D.M. Windsor), pp. 123–133. Smithsonian Institution Press, Washington, DC.
- Coley, P.D. (1983) Herbivory and defensive characteristics of tree species in a lowland tropical forest. *Ecological Monographs*, **53**, 209–233.
- Coley, P.D. (1986) Costs and benefits of defense by tannins in a neotropical tree. *Oecologia*, **70**, 238–241.
- Connell, J.H. & Lowman, M.D. (1989) Low diversity tropical and subtropical rainforests – some possible mechanisms for their existence. *American Naturalist*, **134**, 88–119.
- Ewel, J.J. (1976) Litter fall and leaf decomposition in a tropical forest succession in eastern Guatemala. *Journal of Ecology*, **64**, 293–308.
- Elton, C.S. (1973) The structure of invertebrate populations inside neotropical rain forests. *Journal of Animal Ecology*, **42**, 55–104.
- Floyd, A.G. (1990) *New South Wales Rain Forest Trees*. Forestry Commission, NSW; Australian Government Printing Service, Canberra.
- Francis, W.D. (1970) *Australian Rain Forest Trees*. Australian Government Printing Service, Canberra.
- Frankie, G.W., Baker, H.G. & Opler, P.A. (1974) Comparative phenological studies of trees in tropical wet and dry forest in the lowlands of Costa Rica. *Journal of Ecology*, **62**, 881–919.
- Hairton, N.G., Smith, F.E. & Slobodkin, L.B. (1960) Community structure, population control, and competition. *American Naturalist*, **94**, 421–425.
- Hladik, A. (1978) Phenology of leaf production in rain forest of Gabon: distribution and composition of food for folivores. *The Ecology of Arboreal Folivores* (ed. G.G. Montgomery), pp. 51–73. Smithsonian Institution Press, Washington, DC.
- Jordan, C.F. (1971) Productivity of a tropical forest and its relation to a world pattern of energy storage. *Journal of Ecology*, **59**, 127–142.
- Kikuzawa, K. (1983) Leaf survival of woody plant in deciduous broad-leaved forests. 1. Tall trees. *Canadian Journal of Botany*, **61**, 2133–2139.
- Landsberg, J. & Ohmart, C.P. (1990) Defoliation in Australian forests. *Trends in Ecology and Evolution*, **2**, 24–28.
- Larcher, W. (1975) *Physiological Plant Ecology*. Springer, New York.
- Leigh, E.G. & Windsor, D.M. (1982) Forest production and regulation of primary consumers on Barro Colorado Island. *The Ecology of a Tropical Forest* (eds E.G. Leigh, A.S. Rand & D.M. Windsor), pp. 109–123. Smithsonian Institution Press, Washington, DC.
- Leith, H. (ed.) (1974) *Phenology and Seasonality Modelling*. Springer, New York.
- Lowman, M.D. (1982a) *Leaf growth dynamics and herbivory in Australian rain forest canopies*. PhD thesis, University of Sydney, Sydney.
- Lowman, M.D. (1982b) Seasonal variation in insect abundance among three Australian rain forests, with particular reference to phytophagous types. *Australian Journal of Ecology*, **7**, 353–361.
- Lowman, M.D. (1984) An assessment of techniques for measuring herbivory: is rainforest defoliation more intense than we thought? *Biotropica*, **16**, 264–268.
- Lowman, M.D. (1985) Temporal and spatial variability in insect grazing of the canopies of five Australian rainforest tree species. *Australian Journal of Ecology*, **10**, 7–24.
- Lowman, M.D. (1986) Light interception and its relation to structural differences in three Australian rainforest canopies. *Australian Journal of Ecology*, **11**, 163–170.
- Lowman, M.D. (1987) Relationships between leaf growth and holes caused by herbivores. *Australian Journal of Ecology*, **12**, 189–192.
- Lowman, M.D. (1988) Litterfall and leaf decay in three Australian rain forests. *Journal of Ecology*, **76**, 451–465.
- Lowman, M.D. & Box, J.D. (1983) Variation in leaf toughness and phenolic content among five species of Australian rain forest trees. *Australian Journal of Ecology*, **8**, 17–25.
- Medway, L. (1972) Phenology of a tropical rain forest in Malaya. *Biological Journal of the Linnean Society*, **4**, 117–146.
- Mitchell, A. (1982) *The Roof of the Forest – Accessing the Rainforest Canopy*. Williams Collins, Glasgow.
- Molisch, H. (1928) *The Longevity of Plants*. E.H. Fulling, New York.
- Nadkarni, N. (1984) Epiphyte biomass and nutrient capital of a neotropical elfin forest. *Biotropica*, **16**, 249–256.
- Nicholson, P.B., Bockock, K.L. & Heal, O.W. (1966) Studies on the decomposition of the faecal pellets of a millipede (*Glomeria marinata* (Villers)). *Journal of Ecology*, **54**, 755–766.
- Odum, H.T. & Ruiz-Reyes, J. (1970) Holes in leaves and the grazing control mechanism. *A Tropical Rain Forest* (eds H.T. Odum & R.F. Pigeon), pp. 1–69–1–80. US Atomic Energy Commission, Oak Ridge, Tenn.
- Olsen, M.F. (1990) *Aspects of the ecology and physiology of rainforest systems following large scale natural disturbance*. PhD thesis, University of Queensland, Australia.
- Perry, D.R. (1978) A method of access into the crowns of emergent and canopy trees. *Biotropica*, **10**, 155–157.
- Petrie, J.M. (1906) The stinging property of the giant nettle tree (*Laportea gigas* Wedd.). *Proceedings of the Linnean Society of New South Wales*, **31**, 530–545.
- Reich, P.B., Uhl, C., Walters, M.B. & Ellsworth, D.S. (1991) Leaf lifespan as a determinant of leaf structure and function among 23 Amazonian tree species. *Oecologia*, **86**, 16–24.
- Richards, P.W. (1952) *The Tropical Rain Forest*. Cambridge University Press, Cambridge.
- Selman, B. & Lowman, M.D. (1983) The biology and herbivory rates of *Novacastria nothofagi* Selman (Coleoptera: Chrysomelidae), a new genus and species on *Nothofagus moorei* in Australian temperate rain forests. *Australian Journal of Zoology*, **31**, 179–191.
- Sharik, T.L. & Barnes, B.V. (1976) Phenology of shoot growth among diverse populations of yellow birch (*Betula allegheniensis*) and sweet birch (*B. lenta*). *Canadian Journal of Botany*, **54**, 2122–2129.
- Snedecor, G.W. & Cochran, W.G. (1967) *Statistical Methods*, 6th edn. University of Iowa Press, Iowa.
- Webb, L.J. (1959) A physiognomic classification of Australian rain forests. *Journal of Ecology*, **47**, 551–570.
- Webb, L.J., Tracey, J.G. & Williams, W.T. (1972) Regeneration and pattern in the subtropical rainforest. *Journal of Ecology*, **60**, 675–695.

- Whitham, T.G. (1981) Individual trees at heterogeneous environments: adaptation to herbivory or epigenetic noise? *Species and Life History Patterns: Geographic and Habitat Variations* (eds R.F. Denno & H. Dingle), pp. 9–27. Springer, New York.
- Whitmore, T.C. (1984) *Tropical Rain Forests of the Far East*, 2nd edn. Clarendon Press, Oxford.
- Wiegert, R.C. (1970) Effects of ionizing radiation on leaf fall, decomposition, and litter microarthropods of a montane forest. *A Tropical Rain Forest* (eds H.T. Odum & R.F. Pigeon), pp. H-89–H-100. US Atomic Energy Commission, Oak Ridge, Tenn.
- Williams, A.G. & Whitham, T.G. (1986) Premature leaf abscission: an induced plant defense against gall aphids. *Ecology*, **67**, 1619–1627.
- Wint, G.R.W. (1983) Leaf damage in tropical rain forest canopies. *Tropical Rain Forest: Ecology and Management* (eds S.L. Sutton, T.C. Whitmore & A.C. Chadwick), pp. 229–240. Blackwell Scientific Publications, Oxford.
- Wolda, H. (1982) Seasonality of Homoptera on Barro Colorado Island. *The Ecology of a Tropical Forest* (eds E.G. Leigh, A.S. Rand & D.M. Windsor), pp. 319–331. Smithsonian Institution Press, Washington, DC.
- Wong, M., Wright, S.J., Hubbell, S.P. & Foster, R.B. (1990) The spatial pattern and reproductive consequences of outbreak defoliation in *Quararibea asterolepis*, a tropical tree. *Journal of Ecology*, **78**, 579–588.

Received 18 January 1990; revision received 13 January 1992