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LITTERFALL AND LEAF DECAY IN THREE AUSTRALIAN RAINFOREST FORMATIONS

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SUMMARY

(1) Litterfall was measured monthly over five years (1979–84) in three representative rainforest formations of New South Wales, Australia. Known weights of leaf material of selected canopy tree species were laid out on the forest floor in mesh bags and weighed monthly to determine relative rates of leaf decay.

(2) Mean annual litterfall was 6·2 (±0·22), 7·3 (±0·57), and 10·0 (±0·74) t ha^{-1} for cool temperate (microphyll fern forest or MFF), warm temperate (simple notophyll vine forest or SNVF), and subtropical (complex notophyll vine forest or CNVF) rainforests, respectively, with an average of 7·4 t ha^{-1} for rainforests in New South Wales.

(3) Litter caught in traps was sorted into major components of leaf material, wood and reproductive parts for two years to determine proportions of each component and to quantify the seasonal patterns of the canopy. Leaf material averaged 54% over all years and sites, with 35% wood and 11% reproductive parts. MFF exhibited bimodal peaks of leaf-fall in autumn (March–June) and spring (September–October), while CNVF canopies showed a summer leaf-fall peak (November–December), and SNVF had an early summer (October–December) leaf-fall peak.

(4) Multiple analyses of variance were performed on the data to analyse a range of spatial and temporal factors affecting litterfall measurements. In some cases, estimates of litterfall were significantly affected by presence of overhanging subcanopy branches, closeness to tree trunks, and species of canopy tree overhead. Litterfall did not vary with placement of traps between rainforest patches, under different sides of one tree, at different distances away from the trunk of one tree (albeit under its canopy) or among individuals of the same canopy species.

(5) Australian rainforest trees exhibited variability in rates of leaf decay, ranging from less than six months for complete leaf decay in *Dendrocnide excelsa* to over three years for *Nothofagus moorei*.

(6) The differences in litterfall and leaf decay rates are discussed in relation to differences in biomass, seasonality, and activities of canopy-associated fauna of these rainforest formations.

INTRODUCTION

Litterfall collection is a standard non-destructive technique for assessing the productivity, phenology, and turnover of biomass in a forest (Newbould 1967). Litterfall measurements range from 0·6 t ha^{-1} y^{-1} in arctic tundra (Levina 1960) to 25·4 t ha^{-1} y^{-1} in tropical lowland forests (reviewed in Bray & Gorham 1964; Golley 1978). In particular, the amount of leaf material falling reflects a forest's productivity. Rainforests, with their dense leafy canopies, are considered highly productive plant communities, and have relatively high litterfall (e.g. Proctor *et al.* 1983).

Australian rainforests are distributed discontinuously down the eastern side of the mainland from Cape York, Queensland to Cape Otway, Victoria, in areas with at least 1300 mm annual rainfall that extend no further inland than 150 km (Webb 1959; Francis 1981). There are four major rainforest formations in Australia, varying with latitude, altitude, and environmental conditions. Tropical rainforest is restricted to North Queensland. Subtropical rainforest extends from southern Queensland down to central New South Wales in warm, moist pockets often associated with rich, basaltic soils. Temperate rainforests occur throughout New South Wales, Victoria, and Tasmania: warm temperate forests on sites with lower rainfall and poorer soils than required for subtropical forests; and cool temperate forests in cooler, often montane, regions. Within these four general rainforest formations, there are further types defined by botanic or environmental characteristics (Webb 1959).

The litterfall of Australian tropical rainforests in Queensland was estimated as 9·25 t ha^{-1} h^{-1} (Brasell, Unwin & Stocker 1980), and from 7·28 to 10·53 t ha^{-1} y^{-1} (Spain 1984). Similar studies have never been conducted in the other three rainforest formations further south in Australia, although leaf litter alone has been measured and its mineral content analysed (Webb *et al.* 1969). As part of extensive research on leaf growth dynamics of Australian rainforest canopies (Lowman 1982), litterfall and leaf decay rates of subtropical, and warm and cool temperate rainforests were measured. Leaf growth and herbivory levels are reported elsewhere (Lowman 1982, 1984, 1985); leaf senescence and decomposition, the final stages in the turnover of photosynthetic biomass in forests, are reported here.

Studies of litterfall underestimate the biomass of a stand, however, if the leaf portions eaten by herbivores are not also taken into account (Jordan 1971; Lowman 1984). This failure to account for leaf material consumed by herbivores represents only one of several potential errors in using litterfall studies to estimate productivity. Different published studies exhibit considerable methodological variation in sizes and materials, and numbers and placement of traps in sites sampled; duration of collecting period; and categories of litter sorted (reviewed by Proctor 1983). This makes comparison of data from different studies difficult. Similarly, measurements of litter decay rates have their associated methodological problems (Anderson & Swift 1983).

The aim of this study was to quantify and compare litterfall and leaf decay in three of the four major formations of Australian rainforest. To place the comparisons on a sound basis, variation in results from different methods of using litter traps was critically examined, including variation in measurements of litterfall with trap placement and with month and year.

MATERIALS AND METHODS

Location of rainforests

Litter was collected over a five-year period (March 1979–February 1984) in three formations of rainforest in New South Wales, Australia, and leaf decay rates were measured over two years (1980–1982). Sites included New England National Park at 30° 30′S (cool temperate or microphyll fern forest, MFF, dominated by *Nothofagus moorei* F. Muell.); Royal National Park at 34° 10′S and Dorrigo National Park, Never Never Region at 30° 20′S (warm temperate or simple notophyll vine forest, SNVF, including *Ceratopetalum apetalum* D. Don, *Doryphora sassafras* Endl., *Ackmena smithii* (Puir.) Merrill et Perry and others in the canopy); and Dorrigo National Park at 30° 20′ and Mt Keira Reserve at 34° 30′S (subtropical or complex notophyll vine forest, CNVF, with *Dendrocnide excelsa* (Wedd.) Chew, *Doryphora sassafras*, *Sloanea* sp., *Ficus* sp., *Orites excelsa* R.Br., and many others in the canopy). Forest classifications follow the nomenclature of Webb (1959), who also described the floristic and physical environment associated with each. Site descriptions are summarized in Table 1, but listed in greater detail elsewhere (Lowman 1982).

Litterfall measurements

At least twelve litter traps were placed under mature canopies in representative sites of each of the three types of rainforest formation. Trap placement was random, except in cases where specific factors of variability in litter trap placement were being tested in addition to the general study of litterfall. For example, four traps in the CNVF were placed under different sides of *Dendrocnide excelsa* to compare differences in litterfall weights with direction (N, S, E, W of the trunk) of trap placement. In addition, traps were replicated under the canopies of five species (*Nothofagus moorei*, *Toona australis* F. Muell, *Doryphora sassafras*, *Ceratopetalum apetalum*, and *D. excelsa*) to quantify their phenological events. Traps of 1 m^2 dimension were constructed of strong nylon mesh suspended on frames of plastic conduit tubing approximately 0·5 m above ground. Litter was collected monthly, and litter weights were corrected to thirty-day intervals in cases where wet weather prevented collection on the thirtieth day. All litter from each trap was collected in paper bags, and returned immediately to the laboratory, where it was dried (85 °C for at least 48 h), sorted, redried, and weighed. During the first two years (March 1979–February 1981), litter from each trap was sorted monthly into the components of wood, reproductive parts (fruits and flowers), and leaves. Wood comprised all branch sizes, including one event of a large treefall: the section falling across the trap was sawed, dried and weighed. Small portions of 'trash' that accumulated on the bottoms of traps were allocated to the 'wood' component, because it appeared to be shattered sections of woody material; this trash was always $< 5\%$ of total litter weight, although higher proportions have been obtained elsewhere (Proctor *et al.* 1983). Leaf material was further sorted by species to determine the leafing phenologies of certain canopy trees growing in proximity to each trap. During the third and fourth years (March 1981–February 1983), litter from each trap was not sorted but was simply dried and weighed each month. During the fifth year (March 1983–February 1984), litter was collected sporadically, so

TABLE 1. Summary of descriptive characteristics of the rainforest sites studied.

Site	Forest type	Latitude	Altitude (m)	Mean annual rainfall (mm)	Maximum canopy height (m)	Stand density*	Stand diversity
New England National Park	MFF	30°30′S	1200	2000†	40	70	12
Royal National Park	SNVF	34°10′S	20	1302†	33	69	14
Dorrigo National Park							
Never Never Region	SNVF	30°20′S	800	2004§	35	—	—
Glade Region	CNVF	30°20′S	800	2004§	41	65	18
Mt Keira Reserve	CNVF	34°30′S	400	1302‡	42	63	15

* Number of individual trees (> 1 m height) and species as measured in a 525 m^2 plot, 70 m × 7·5 m (see Lowman 1986 for illustrations of these profile diagrams).

† Roger Hacking, Ranger, personal communication.

‡ Records from town of Waterfall meteorological station.

§ Records from town of Dorrigo meteorological station; see Lowman 1982 for monthly weather data at each site.

only the total annual litter per trap was calculated. From these sorting regimes, both seasonal and annual comparisons of the temporal variation in litterfall were examined.

Comparisons of litterfall with different trap placements

In addition to seasonal analyses of litterfall, various types of spatial variation in litterfall were examined:

(a) Large-scale site differences in litterfall, both between different rainforest formations (MFF, SNVF, and CNVF) and between similar rainforest formations (two sites of SNVF) in different geographic regions of New South Wales.

(b) Small-scale site differences in litterfall (between three pockets of MFF that were isolated but within 5 km of one another).

(c) Differences in litterfall in relation to positions of nearby trees: (i) placement of litter traps in relation to distance from tree trunks (1 m, 3 m and 5 m intervals from bole of *D. sassafras* in SNVF, Royal); (ii) placement of litter traps in relation to aspect around tree trunks (N, S, E, W around *D. excelsa* in CNVF, Dorrigo); and (iii) placement of traps adjacent to *N. moorei* trees vs. not adjacent to trees in the cool temperate rain forest (MFF).

(d) Trap placement in relation to the canopy directly above: (i) closeness of overhanging branches (low vs. high overhanging branches in the MFF and the CNVF); (ii) species of tree overhanging a litter trap (*D. excelsa* vs. *T. australis* vs. *D. sassafras* in CNVF; *D. sassafras* vs. *N. moorei* in MFF); and (iii) traps under different individuals of one species (three *T. australis*, three *D. sassafras* and three *D. excelsa* trees in the CNVF; three *N. moorei* and three *D. sassafras* trees in the MFF).

Monthly dry weights (g) of litter from each trap were analysed for variability using analyses of variance and the significant differences ranked by Student–Newman–Keuls ranking procedure. Cochran's test was used prior to analyses to determine homogeneity of variance; where necessary, data were transformed to log $(x+1)$.

Leaf decay measurements

Leaf decay rates were measured for five species: *Nothofagus moorei* and *Doryphora sassafras*, the dominant canopy and a common understorey species, respectively, in the MFF; *D. sassafras* and *Ceratopetalum apetalum*, common canopy trees in the SNVF; and *D. sassafras*, *Dendrocnide excelsa*, and *Toona australis* in the CNVF canopy. More detailed information on the leaf growth, herbivory, and abscission in these species is listed elsewhere (Lowman 1982, 1984).

For each species in each rainforest formation, thirty plastic mesh bags (5 mm^2 mesh) were placed on the forest floor, each containing 30 g fresh weight of old leaves. Leaves were picked from the basal section of branches in the canopy (i.e. shade leaves), and were judged to be old by their position on the branch, the presence of epiphylly or of reddening yellowing pigmentation, and corresponded to 'age class 5' when analysed for leaf chemicals and toughness (Lowman & Box 1983). Three bags per species per site were collected each month for eight months; and the last two collections were made at two-monthly intervals so the final (tenth) collection occurred exactly one year after commencement of the experiment. The leaf material in each mesh bag collected was transferred to a paper bag, and returned to the laboratory immediately, where it was dried at 85 °C for 24 h, and weighed. Three bags of each leaf treatment were dried and weighed at the commencement of the experiment, to serve as the initial sample standard (i.e. 0%

leaf decay). The dry weights were then transformed into percentage loss based upon the initial sample weights, which represented 100% leaf material.

The entire field design was repeated over two time intervals (commencing in September 1980 and in January 1981) to test for seasonality in the activity of decomposers as reflected by time of initiation of leaf decay. In addition, both old (>2 years old; age class 5) and mature (1 year old; age class 3; Lowman & Box 1983) leaves of *C. apetalum* were tested separately and compared in the SNVF (Royal). Species were tested in at least two sites where possible, both of which represented their natural distribution: *T. australis* and *D. excelsa* in CNVF (Royal) and SNVF (Dorrigo); *D. sassafras* in MMF (New England), SNVF (Royal), and CNVF (Dorrigo); *C. apetalum* in SNVF (Royal); and *N. moorei* in MFF (New England). Since shade leaves were used in all cases, it is assumed that the resulting decay rates are faster than would be obtained for sun leaves, which are tougher and thicker (Lowman & Box 1983).

RESULTS

Litterfall measurements

Average annual litterfall

The mean total litterfall for all rain forest sites in New South Wales, Australia was 7·4 t ha^{-1} y^{-1} (Table 2). Total litterfall weights (t ha^{-1} y^{-1}) ranged from as high as 10·0 (±0·74) in the CNVF, to 7·3 (±0·57), 5·4 (±0·43) and 6·2 (±0·22) in SNVF (Royal), SNVF (Dorrigo), and MFF, respectively. The greatest litterfall occurred in the most complex rainforest type studied (CNVF), which has a higher and more extensive canopy area than either the SNVF or the MFF (Table 1, see also Lowman 1986). Despite the relatively long duration of litter collections, total litterfall was nonetheless significantly different among the four years for each rainforest formation (CNVF: $F_{11,36}=7{\cdot}22$; SNVF: $F_{8,27}=5{\cdot}38$; MFF: $F_{11,36}=2{\cdot}73$, $P<0{\cdot}05$), probably because different annual rainfall and

TABLE 2. Average dry weights (t ha^{-1} y^{-1}) of litterfall at four rainforest sites in New South Wales, Australia.

Site	Litterfall component (±S.E.) Leaf* (% Litter component)	Wood*	Fruit*	Total†
New England National Park, MMF	3·7 (0·7) (53%)	3·0 (0·54) (43%)	0·3 (0·30) (4%)	6·2 (0·22)
Royal National Park SNVF	4·1 (0·21) (53%)	2·3 (0·17) (30%)	1·3 (0·12) (17%)	7·3 (0·57)
Dorrigo National Park, Never Never Region, SNVF	2·9 (0·19) (54%)	1·8 (0·12) (33%)	0·7 (0·11) (13%)	5·4 (0·43)
Dorrigo National Park, CNVF	5·4 (0·19) (54%)	3·2 (0·21) (32%)	1·4 (0·19) (14%)	10·0 (0·74)
All sites, average	4·0 (54%)	2·6 (35%)	0·8 (11%)	7·4 (100%)

* Calculated from first two years; collection at monthly intervals; litter components were not sorted during third and fourth years of measurement ($n=24$ for each rainforest formation).

† Calculated from four years' collection at monthly intervals so does not exactly represent total of first three columns ($n=48$ for each rainforest formation).

storm patterns led to different intensities of wood fall (see Lowman 1982 for more detailed weather data).

The litterfall components comprised an average of 54% leaf material, 35% wood and 11% fruit (Table 2). These proportions were consistent for leaf material among the different sites, but varied slightly for wood and fruit. Woodfall ranged from only 30–33% in the SNVF sites, to 43% in the MFF whose montane location is characterized by high winds and storms, resulting in relatively frequent branch and treefall. Fruitfall, however, was low in the MFF (only 4%), where the predominant canopy tree (*Nothofagus moorei*) is a mast-seeder producing reproductive parts only every 3–5 years. This occurred during spring 1980, whereas fruitfall was negligible in the MFF during the other three years. In contrast, the CNVF and SNVF litter comprised 13–17% fruit material; these sites have many canopy species that reproduce annually, some with heavy, fleshy fruits.

Mean leaf-fall was 4 t ha^{-1} y^{-1} for all sites, but ranged from as high as 5·4 t in the CNVF to less than half that (2·09 t) in the SNVF site only 10 km away on the edge of the escarpment. Mean woodfall was 2·6 t ha^{-1} y^{-1} although its associated standard errors were relatively high. Trunk or large branchfall into or across the traps, albeit relatively infrequent, did occur and resulted in high variability between monthly collections. Woodfall was highest in the CNVF, at 3·2 t ha^{-1} y^{-1}, and lowest in the Dorrigo SNVF site, with only 1·8 t. The proportion of wood was highest in the MFF, however, where the annual fall of 3·0 t comprised 43% of total litterfall, discussed above. Fruitfall averaged 0·8 t ha^{-1} y^{-1} in all New South Wales sites sampled, ranging from 1·4 t in the CNVF to only 0·3 t in the MFF.

Litterfall weights were compared within and between the three main types of rainforest formation: MFF, SNVF, and CNVF in increasing order of complexity (Table 3). Litterfall and each of its three components—leaf, wood and fruit—were highly significantly different ($P<0·001$) between the three formations, and were highest in the CNVF in all four litter components. Within the sites, however, total litter and wood were not significantly different between traps at three of the four rainforests analysed. In contrast, fruit and leaf litter varied significantly between traps in three out of four sites, most likely a consequence of trap placement: fruit and leaf-fall varied according to tree species above each trap, whereas wood and total litter were fairly constant between traps.

TABLE 3. Comparisons of litterfall (total litter, leaf, wood, and fruit) (t ha^{-1}) within and between four rainforest regions in New South Wales, Australia. See text for explanation of site initials.

Litter component	Within sites: MFF	SNVF (Royal)	SNVF (Dorrigo)	CNVF	Between sites
Total litter	1·21 N.S.	15·30***	3·86 N.S.	1·19 N.S.	40·44***
Leaf	22·96***	63·80***	0·11 N.S.	12·46***	23·23***
Wood	0·94 N.S.	408·80***	1·17 N.S.	0·83 N.S.	19·37***
Fruit	6·37**	11·07**	0·49 N.S.	18·11***	28·61***

N.S. non-significant.
* $P<0·05$.
** $P<0·01$.
*** $P<0·001$.

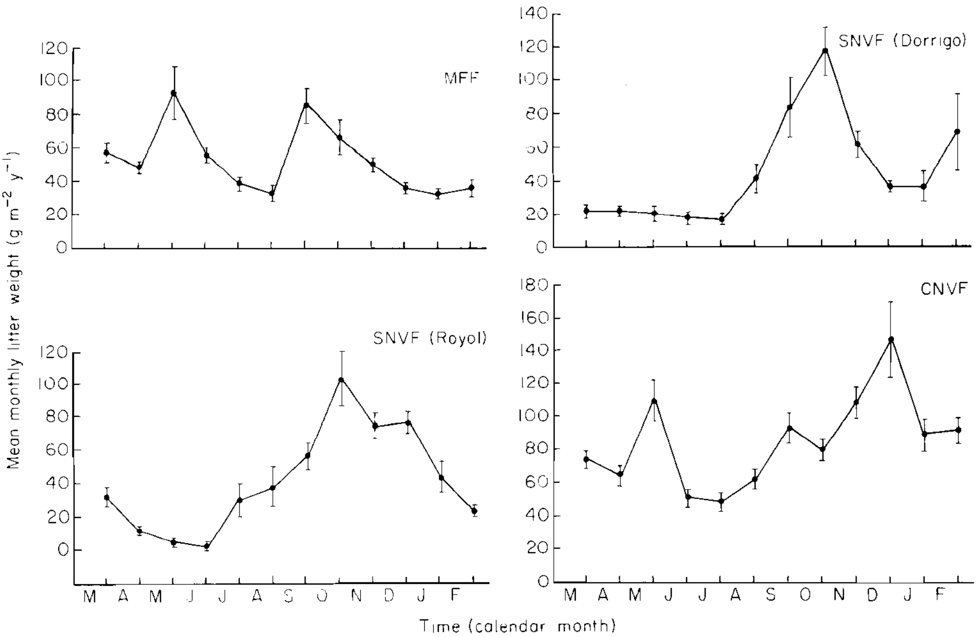

FIG. 1. Litterfall (mean weight per site $\pm$ 1 S.E. g m^{-2} y^{-1}) in four rainforest sites, New South Wales, Australia: MFF, microphyll fern forest; SNVF (Royal) and SNVF (Dorrigo), simple notophyll vine forests in Royal and Dorrigo National Parks; and CNVF, complex notophyll vine forest. Each point represents a monthly mean calculated from four (MFF, CNVF) or three (SNVF) years' litter collections.

Seasonal fluctuations in litterfall

All four rainforests had bimodal peaks in their annual patterns of litterfall, but with different seasonal fluctuations (Fig. 1a–d). In the MFF, litterfall peaked during autumn (May) and spring (September–October), while in both SNVF sites, the maximum fall occurred during spring (October) with a lesser summer peak in November–December (Royal) or February (Dorrigo). The CNVF exhibited highest litterfall during early summer (December), with a smaller peak during autumn (May).

The seasonality of each component of litterfall was also quantified, but only over a two-year span (Fig. 2 a–d). These graphs reveal that not all of the total litterfall peaks (Fig. 1 a–d) were composed of consistent proportions of leaf, wood and reproductive matter. Furthermore, the peaks composed of wood (as a result of a tree or large branchfall) were not annually repeated patterns, but random events.

In the MFF, leaf-fall was highest during autumn (May–June) and during spring (September–October) (Fig. 2a). Because the MFF canopy is predominantly *Nothofagus moorei*, the litter patterns closely parallel the phenology of this species. This bimodal pattern of leaf-fall is typical of many evergreen temperate trees: a portion of the canopy abscises immediately before the winter months, and another portion falls simultaneously as new leaves flush in the spring. In total, approximately half the canopy was shed annually, leaf longevity of *N. moorei* being approximately two years (Lowman 1982). The high woodfall in May reflects the heavy rains and storms that consistently occurred during autumn, causing both tree and large branchfalls into the litter traps. Fruitfall was relatively low in the MFF. The majority of reproductive parts collected in the litter traps were from vines, epiphytes and understorey such as *Elaeocarpus holopetalus* F. Muell. and *D. sassafras*. The peak during September–October, however, resulted from the flowering and fruiting of beech during 1980. As a mast-seeder, beech trees only flower every three to five years; the reproductive litter weights of beech were negligible in other years.

Both SNVF sites had similar patterns of spring leaf-fall (Fig. 2 b,c) but the peaks were slightly later in the more southerly site (October–December in Royal as compared to September–October in Dorrigo, 500 km to the north). Leaf abscission times coincided with the months of major leaf-flushing activities of most canopy trees in these rainforest sites (Lowman 1982). The shedding of bark and branches was heaviest during spring and summer, with very little wood falling during the autumn and winter. No large treefalls occurred in the vicinity of the SNVF litter traps during 1979–81, so the annual pattern was fairly homogeneous. Fruitfall peaked in August at Royal (due in part to the successful flowering in 1980 of lilly pilly, *Acmena smithii*, which has a heavy, fleshy fruit). Fruitfall in Dorrigo peaked during February, here again reflecting the phenology of a canopy species with large, fleshy fruits (*Endiandra introrsa* C.T. White, Dorrigo plum).

The seasonal patterns of leaf-fall in the CNVF (Fig. 2d) peaked during spring–summer (September–December), a time which coincided with the leaf flush of most canopy trees. The smaller leaf peak in May was due to a deciduous species *Toona australis* that lost its entire canopy during autumn. (More information on leaf-fall of individual species whose canopies were above the litter traps is given below.) Woodfall peaked in May, a result of the heavy rainstorms that caused tree and large branchfalls (the same storms that affected woodfall in MFF). Woodfall throughout the rest of the year consisted mainly of small branches and bark flecks. Litterfall of reproductive parts was sporadic (albeit higher than in any other rainforest formation), with peaks during periods of fruitfall of species with fleshy fruits. They included *Endiandra introrsa* during February–March; *Brachychiton acerifolium* (A. Cunn. ex Don) F. Muell. (flowers) during November–January; *Toona australis* in March; *Cryptocarya glaucescens* R.Br., *Geoissos benthamii* F. Muell. and *Sloanea australis* (Benth.) F. Muell. in April; *C. apetalum* (flowers) and *Ficus macrophylla* Desf. ex Planch. fruits in January; *D. sassafras* (flowers) in June; and *Acmena smithii* fruits in August.

Statistical differences in litterfall weights were tested between the four seasons (analyses of variance among months were not valid, because monthly trap weights were not independent), using months as replicates of a given season. At all sites, litterfall was significantly highest in the spring and lowest in the winter (MMF, $F_{3,320} = 11{\cdot}09$; SNVF, $F_{3,320} = 58{\cdot}17$; and CNVF, $F_{3,320} = 46{\cdot}85$, $P < 0{\cdot}001$).

Comparisons of litterfall in relation to placement of litter traps

Nearness to tree trunks. Litter weights from traps situated on different sides (N, S, E, W) of trees of *D. excelsa* in the CNFV were statistically similar for all litter components. In the closed canopy environment of the CNVF, prevailing winds did not appear to alter the direction of falling litter. Secondly, traps situated at different distances from tree trunks (1 m, 3 m, 5 m away from *D. sassafras* in SNVF) showed no significant difference in weights of any litter component. The trap nearest to the tree trunk did not accumulate heavier litter weights from the dense canopy above, nor did litter appear to be deflected away from the trap by the nearby trunk. Thirdly, litterfall was compared between traps placed adjacent to tree trunks (*N. moorei*) and traps placed in the open away from tree trunks,

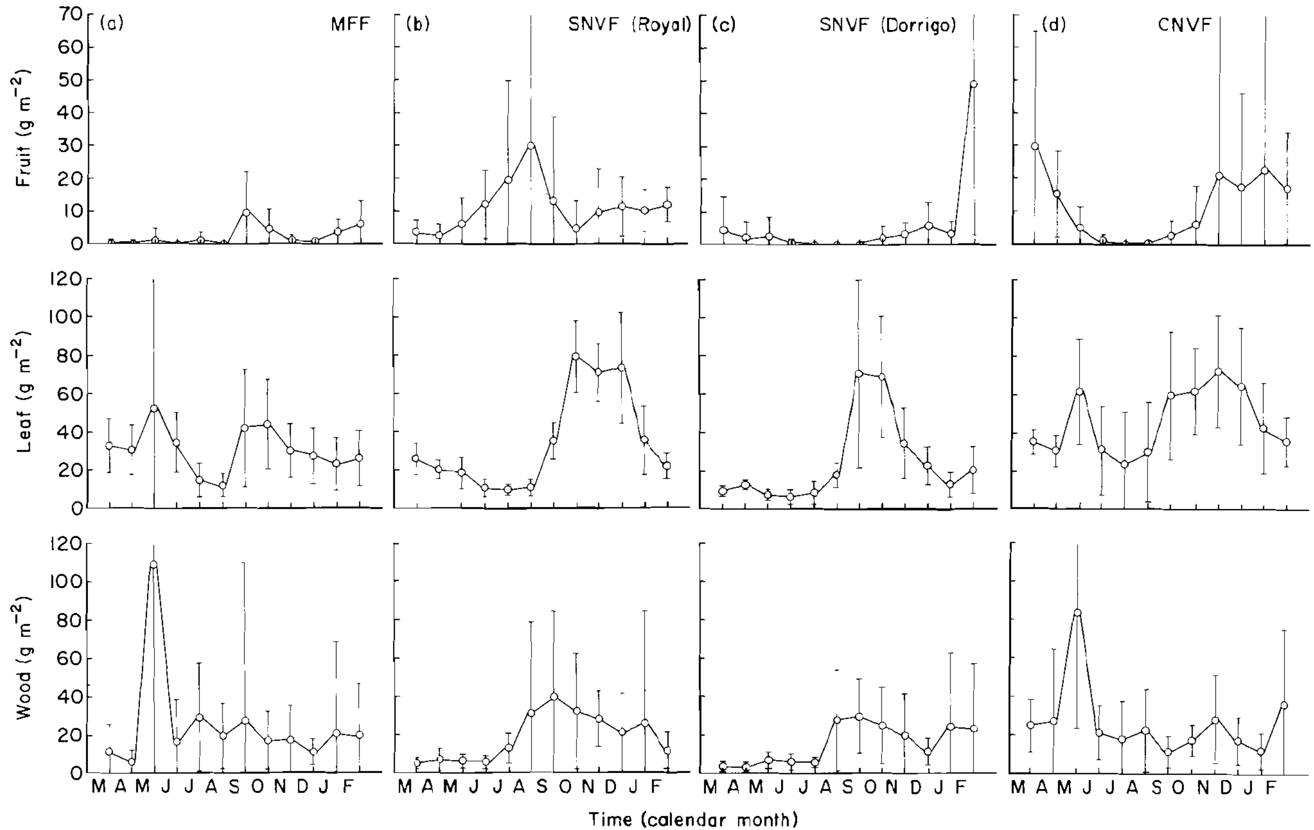

FIG. 2. Litter falling monthly as fruit, wood and leaf in four rainforest sites in New South Wales: (a) MFF (mossy microphyll forest); (b) SNVF Royal (simple notophyll vine forest); (c) SNVF Dorrigo; and (d) CNFV (complex notophyll vine forest). Monthly amounts are expressed as $g\,m^{-2} \pm 2$ S.D., and represent the average of two years' collection.

albeit within the same forest canopy. Both woodfall and *N. moorei* leaf-fall were homogeneous in this test, but fruit and total leaf-fall varied significantly with distance from the trunk. The heaviest (wood) and most homogeneous (*N. moorei* leaves) litter components were unaffected by trap placement in relation to tree trunks, but fruit and leaves of other species fell more heavily into traps located away from tree trunks.

Canopy above trap. Litter traps placed under low, overhanging subcanopy branches showed little significant difference as compared to traps not under low overhanging branches. In the MFF, all components of litterfall were homogeneous whether the trap was situated under subcanopy branches or not, ($F_{1,360}=2{\cdot}66$, N.S.). In the CNVF, however, leaves and fruits fell homogeneously, regardless of presence or absence of overhanging subcanopy branches ($F_{1,168}=0{\cdot}15$; $F_{1,168}=3{\cdot}46$; both N.S.); but wood was deflected so that significantly less fell into traps beneath overhanging branches ($F_{1,168}=10{\cdot}15$, $P<0{\cdot}01$) as compared to traps under open subcanopy.

Litterfall varied markedly in traps under different species of canopy trees. In the MFF, traps under *D. sassafras* collected less total litter than under *N. moorei* ($F_{1,264}=8{\cdot}50$, $P<0{\cdot}01$). The leaf-fall of each individual species was statistically higher under its own canopy, but the components of fruit and wood were homogeneous. In the CNVF, wood weights were homogeneous between traps placed under the canopies of three species; but fruit, leaves, and total litter varied significantly under different canopy trees.

In most cases, litterfall did not differ significantly among replicate individuals of one canopy tree species. The only exception of this was *D. excelsa*, where all litter components except leaf-fall varied between individuals. These differences probably reflect litterfall of the other trees growing adjacent to the traps since litter components of *D. excelsa* are extremely light, containing proportionally more water weight than for any other rainforest tree measured (Lowman 1982).

In summary, litter traps are inevitably situated under different canopy conditions. Litter weights in the MFF were not affected by presence or absence of subcanopy branches or differences between individual trees, but varied between traps under canopy (*N. moorei*) or subcanopy (e.g. *D. sassafras*) individuals. In the CNVF, litterfall weights varied slightly in relation to presence of overhanging subcanopy branches; and under different species and individuals of canopy trees. The increased complexity of the CNVF appears to require a greater variability in trap placement to assure representative litter collection.

Leaf decay measurements

Leaf decay rates varied considerably among species ranging from as little as four months for *D. excelsa*, to over two years for *N. moorei* (Fig. 3).

D. excelsa leaves decayed very rapidly (Fig. 3a), with over 95% of the original dry weight lost after only four months. The remaining 5% consisted mainly of midveins that required up to eight months to break down. This was the fastest decay rate measured in this study, but perhaps predictable due to the soft, mesomorphic tissue of *D. excelsa* leaves.

Although *T. australis* leaves were not sclerophyllous as are many Australian rainforest trees, they required over one year to decay fully (Fig. 3b). Leaves on the forest floor of the CNVF decayed slightly faster than at the SNVF Royal, probably due to moister, warmer conditions of the former.

C. apetalum leaves also decayed very slowly, requiring almost one year to lose 50% of their initial weight (Fig. 3d). The young leaves (1-year old) decayed slightly faster than did

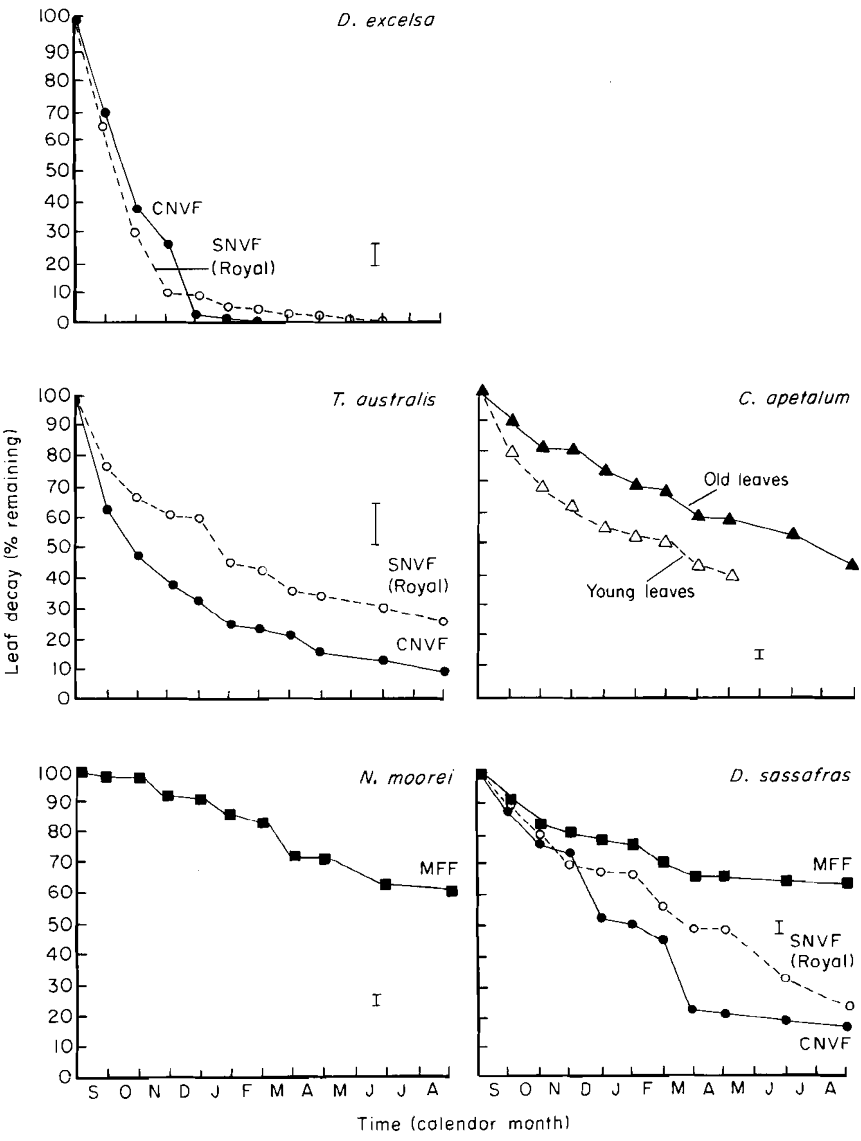

FIG. 3. Leaf decay of five rainforest tree species over one year expressed as percentage remaining of original leaf weight. Sites abbreviated as follows: MMF (mossy microphyll forest); SNVF (simple notophyll vine forest); and CNVF (complex notophyll vine forest); bars = S.E.

the old leaves (≥ 2 years old); but even they were much slower than mature *D. excelsa* leaves.

D. sassafras grew in all three rain forest formations studied, so leaf decay was measured at each site. Its leaves decayed faster in the CNVF habitat than in the MFF, with an intermediate rate in the SNVF, Royal (Fig. 3e). Decay was negligible in the MFF floor during winter, and rates were fastest during summer at all three sites.

N. moorei leaves decayed extremely slowly (Fig. 3c), with over 60% undecayed after one year. Since beech leaf-fall peaked during two different seasons, it was hypothesized that the time of leaf-fall may also affect the decay rates (due perhaps to seasonality of decomposers, temperature, moisture, or to the physical state of leaf tissue at time of abscission). To test for this, the beech decay experiment was conducted over two time intervals, one initiated in August and one in January. A two-way analysis of variance showed differences with respect to both factors. Different months showed significantly different rates of decay ($F = 8{\cdot}77$, $P < 0{\cdot}001$), with summer months exhibiting the fastest rates; the time of initiation of decay was even more significant ($F = 55{\cdot}64$, $P < 0{\cdot}001$), with leaves placed on the forest floor in summer (January) disappearing more rapidly than in winter (August). The significant interaction ($F = 16{\cdot}24$, $P < 0{\cdot}001$) implied that a combination of time of decay initiation and given monthly intervals of decay contributed a large portion to the variability.

DISCUSSION

Variability in litter production

Rainforest litter usually averages between 6 and 12 t ha^{-1} y^{-1} (Bray & Gorham 1964; Golley 1978; Proctor *et al.* 1983), and this study is no exception. The highest litterfall (10·0 t ha^{-1} y^{-1}) occurred in the subtropical CNVF, and the lowest in the MFF or cool temperate rainforest (6·2 t ha^{-1} y^{-1}). Most litter studies in Australian forests have been conducted under eucalypt or dry sclerophyll canopies where litterfall is approximately 3–5 t ha^{-1} y^{-1} (e.g. Ashton 1975; Congdon 1979). In contrast, subtropical Australian mangroves shed an average of 5·8 t ha^{-1} y^{-1} (Goulter & Alloway 1979). A tropical rainforest litter study conducted previously in Australia averaged 9·25 t ha^{-1} y^{-1} (Brasell, Unwin & Stocker 1980). This is surprisingly lower than the litterfall collected in the subtropical forests of this study, but their tropical sites included some *Araucaria cunninghamii* Ait. ex D. Don plantations, and some undisturbed rainforests that were actually belts (*c.* 100 m wide) adjacent to the plantations. Both these factors may have resulted in litterfall that was slightly lower than in a well-developed, undisturbed tropical rainforest. In another study, Spain (1984) measured 7·28–10·53 t ha^{-1} y^{-1} in three Australian tropical rainforest sites. The fact that both of these litterfall studies in Australian tropical rainforests did not have proportionally more litter than in the subtropical and temperate rainforests reported here may be due to the inclusion of large branch and treefall weighted in this study; they are often omitted in litterfall studies. The only extensive litterfall collection in cool temperate rainforests reported weights of 5000 lbs acre^{-1} (5 t ha^{-1}) in New Zealand (Miller & Hurst 1957), similar to this study.

When comparing litterfall among different studies, it is often difficult to account for the potential errors arising from variation in methodology (Proctor 1983). Litter-trap designs (Newbould 1967) vary in size (from <20 cm up to 1 m diameter) (shape from round to square), position (from ground level to >1 m above ground), construction (e.g. plastic ice-cream tubs, wooden boxes, plastic mesh bags suspended on frames), and in function (water proof, animal proof, exclusive to large branches, or inclusive of small reproductive parts). Second, the number and placement of traps greatly affects the reliability of litterfall, as shown in this study. Other reviews of litterfall in the literature have mentioned the need for confidence limits on litterfall results to indicate the variability of averages obtained (Proctor *et al.* 1983). Thirdly, the frequency of collection and duration of study greatly affect the reliability of results obtained. Even in this study, litterfall was significantly variable between four years, probably due to the large differences in wood weights between the years (Table 2). Studies of one year or less simply cannot hope to estimate litter accurately, because of the annual variation in biological (e.g. fruiting and flowering) and physical (e.g. rainfall) factors.

Relationships between leaf litter and herbivory

The amount of leaf material in the litterfall was approximately 54%, which is similar to most other studies, although up to 85% leaf material has been reported in montane rainforests of Jamaica (Tanner 1980). Leaf-fall, when taken in conjunction with leaf longevity, can be used to estimate the canopy biomass, but only if the amounts of leaf surface missing to herbivores have been quantified. Previous studies on defoliation in these rainforest sites estimated leaf area losses at 14·6% in CNVF, 22·0% in SNVF and 26% in MFF (Lowman 1984). If these portions missing to herbivores are added to the litterfall weights, then the estimates of forest biomass are higher: 10·9 t ha^{-1} y^{-1} in the CNVF, and 8·5 t ha^{-1} y^{-1} mean biomass for all rainforests measured in N.S.W., Australia (Table 4). Wood borers and frugivores may also contribute to underestimates of the weights of both wood and reproductive component as measured by the litterfall.

Most other litterfall studies fail to account for portions of leaves missing to herbivores (but see Proctor *et al.* 1983). When litterfall studies are conducted solely to measure the biomass entering the decay pathway on the forest floor, this is acceptable. But if, as with many studies, litterfall measurements are subsequently extrapolated to estimate forest productivity or above-ground biomass or nutrient availability, then the results may underestimate the original canopy present. Further studies on wood and fruit losses to their associated predators before senescence would further quantify the accuracy of measurements of the turnover of plant material through the litterfall pathway.

Leaf decay in Australian rainforests

Decay represents the final phase in the life cycle of a leaf, whereby its constituents are recycled back into the forest system. As with litterfall studies, the methodology for leaf decay studies is extremely variable although relatively few studies have been conducted (Anderson & Swift 1983). Some investigators tether individual leaves to stakes on the forest floor (e.g. Gong & Ong 1983), others lay out disks of leaf material (e.g. Heath & Arnold 1966), and some use mesh bags (e.g. Shanks & Olsen 1961; Ewel 1976; this study).

TABLE 4. Litterfall (t ha^{-1} y^{-1}) at four rainforests in New South Wales, Australia after correcting for leaf area losses to herbivores.

Site*	Herbivory† (% leaf area loss)	Leaf litter weights: Uncorrected	Leaf litter weights: Corrected	Total litter weights: Uncorrected	Total litter weights: Corrected
MFF	26·0	3·7	5·0	6·2	8·3
SNVF (Royal)	22·0	4·1	5·3	7·3	8·9
SNVF (Dorrigo)	22·0	2·9	3·7	5·4	6·2
CNVF	14·6	5·4	6·3	10·0	10·9
All sites, $\bar{x}$	20·9	4·0	5·1	7·4	8·5
(% of total)		(54%)	(60%)	(100%)	(100%)

* See text for site abbreviations.
† See Lowman (1984) for calculations of herbivory levels.

The rates of decay measured in this study were much lower than those for most rainforest trees in the literature, where half-lives of approximately seventy days are reported (Ewel 1976). And even slower decay rates would have been obtained if the leaves had been selected from the upper (sun) rather than the lower (shade) regions of tree canopies, because sun leaves decay more slowly than shade leaves (Heath & Arnold 1966). Australian rainforest trees are mainly sclerophyllous, however, with *N. moorei*, *D. sassafras* and *C. apetalum* all being very tough (Lowman & Box 1983) compared to the mesomorphic leaves of *D. excelsa*. The decay rates appeared to correspond to leaf toughness and tannins, with *N. moorei* (both tough and high in tannins) having the slowest decay and *D. excelsa* (both soft and low in tannins) decaying in less than six months (Lowman & Box 1983). The relatively slow recycling of most leaf material through the decomposer pathway may serve to balance the more rapid re-entry of leaf nutrients through frass (Nicholson, Bocock & Heal 1966), particularly in the MFF rainforests where the beech leaves suffer relatively high defoliation (*c.* 31%) (Lowman 1982; Selman & Lowman 1983) but exhibit slow decay on the forest floor. One of the few studies to measure frass decay rates showed a half-life of one year for faecal pellets of millipedes that ate hazel leaves (*Corylus avellana*) (Nicholson, Bocock & Heal 1966). If the frass of beech herbivores is similar, then the leaf portions passing through herbivores are re-cycling at least twice as fast as leaf material that abscissed. In view of the slow leaf decay rates measured, further studies comparing the recycling of leaf nutrients via direct consumption (herbivores) and indirect consumption (decomposers) would be of greater interest in understanding the importance of litterfall in these rainforests.

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REFERENCES

Anderson, J. M. & Swift, M. J. (1983). Decomposition in tropical forests. *Tropical Rain Forest: Ecology and Management* (Ed by S. L. Sutton, T. C. Whitmore & A. C. Chadwick), pp. 287–311. Blackwell Scientific Publications, Oxford.

Ashton, D. H. (1975). Studies of litterfall in *Eucalyptus regnans* forests. *Australian Journal of Botany*, **23**, 413–433.

Brasell, H. M., Unwin, E. L. & Stocker, G. C. (1980). The quality, temporal distribution and mineral-element content of litterfall in two forest types at two sites in tropical Australia. *Journal of Ecology*, **68**, 123–139.

Bray, J. R. & Gorman, E. (1964). Litter production in forests of the world. *Advances in Ecological Research*, **2**, 101–157.

Congdon, R. A. (1979). Litterfall of the paperback tree (*Melaleuca cuticularis*) in the marshes of the Blackwood River Estuary, Western Australia. *Australian Journal of Ecology*, **4**, 411–417.

Ewel, J. J. (1976). Litter fall and leaf decomposition in a tropical forest succession in eastern Guatemala. *Journal of Ecology*, **64**, 293–308.

Francis, W. D. (1981). *Australian Rain-Forest Trees.* Australian Government Publishing Service, Canberra.

Golley, F. B. (1978). Forest leaf production. *The Ecology of Arboreal Folivores* (Ed by G. G. Montgomery), pp. 17–22. Smithsonian Institution, Washington.

Gong, W. K. & Ong, J. E. (1983). Litter production and decomposition in a coastal hill dipterocarp forest. *Tropical Rain Forest: Ecology and Management* (Ed by S. L. Sutton, T. C. Whitmore & A. C. Chadwick), pp. 275–287. Blackwell Scientific Publications, Oxford.

Goulter, P. F. E. & Alloway, W. G. (1979). Litter fall and decomposition in a mangrove stand, *Avicennia marina* (Forsk.) Vierh., in Middle Harbour, Sydney. *Australian Journal of Marine and Freshwater Research*, **30**, 541–546.

Heath, G. W. & Arnold, M. K. (1966). Studies in leaf-litter breakdown. II. Breakdown rate of 'sun' and shade' leaves. *Pedobiologia*, **6**, 238–243.

Jordan, C. F. (1971). Productivity of a tropical rain forest and its relation to a world pattern of energy storage. *Journal of Ecology*, **59**, 127–142.

Levina, V. I. (1960). Determination of the amount of annual litter fall in two types of pine forest of the Kola Peninsula. *Bot. Zh.* **45**, 418–423 (cited in *Forestry Abstracts* **21**, 532).

Lowman, M. D. (1982). *Leaf growth dynamics and herbivory in Australian rain forest canopies.* Ph.D. thesis, University of Sydney.

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 rain forest canopies. *Australian Journal of Ecology*, **11**, 163–170.

Lowman, M. D. & Box, J. R. (1983). Variation in leaf toughness and phenolic content among five species of Australian rain forest trees. *Australian Journal of Ecology*, **8**, 17–25.

Miller, R. B. & Hurst, F. B. (1957). The quantity and nutrient content of hard beech litter. *New Zealand Forestry Research Notes*, **8.**

Newbould, P. J. (1967). *Methods for Estimating the Primary Production of Forests.* IBP Handbook No. 2. Blackwell Scientific Publications, Oxford.

Nicholson, P. B., Bocock, K. L. & Heal, O. W. (1966). Studies on the decomposition of the faecal pellets of a millipede (*Glomenis marginata* (Villers)). *Journal of Ecology*, **54**, 755–766.

Proctor, J. (1983). Tropical forest litterfall. I. Problems of data comparison. *Tropical Rain Forest: Ecology and Management* (Ed by S. L. Sutton, T. C. Whitmore & A. C. Chadwick), pp. 267–273. Blackwell Scientific Publications, Oxford.

Proctor, J., Anderson, J. M., Fogden, S. C. L. & Vallack, H. W. (1983). Ecological studies of four contrasting lowland rain forests in Gunung Mulu National Park, Sarawak. *Journal of Ecology* **71**, 261–263.

Shanks, R. E. & Olson, J. S. (1961). First-year breakdown of leaf litter in southern Appalachian forests. *Science*, **134**, 194–195.

Selman, B. & Lowman, M. D. (1983). The biology and herbivory rates of *Novacastria nothofagi* Selman (Coleoptera: Chrysomelidae), a new genus and species of *Nothofagus moorei* in Australian temperate rain forests. *Australian Journal of Zoology*, **31**, 179–91.

Spain, A. V. (1984). Litterfall and the standing crop of litter in three tropical Australian rainforests. *Journal of Ecology*, **72**, 947–61.

Tanner, E. V. J. (1980). Litterfall in montane rain forests of Jamaica and its relation to climate. *Journal of Ecology*, **68**, 833–848.

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. & Lance, G. N. (1969). The pattern of mineral return in leaf litter of three subtropical Australian forests. *Australian Forestry*, **33**, 99–110.

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