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Biotropica, Volume 23, Issue 3 (Sep., 1991), 271-281.

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BIOTROPICA 23(3): 271–281 1991

The Spatial Distribution of Herbivory, Mines and Galls within an Australian Rain Forest Tree[1]

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ABSTRACT

The spatial distribution of herbivory, mines and galls was investigated within the crowns of the canopy tree *Argyrodendron actinophyllum* (Sterculiaceae) in a subtropical rain forest near Brisbane, Australia. Apparent leaf damage amounted to 11 percent of leaf area removed, was significantly higher in sun than in shade leaves, was not significantly higher in the upper crown (>25 m) than in the lower crown (15–25 m), and did not differ significantly among compass orientations. Leaf biomass removed by herbivores was significantly higher in the upper crown and in sun samples. Overall leaf damage, including leaflets entirely eaten and leaf-mining, ranged from 11 percent to 19 percent. However, actual leaf consumption was mainly restricted to young leaves, and amounted to about 16 percent; this was more dependent on the location of isolated, abundant, and sunny patches of young foliage than on local differences in foliar nutrient characteristics, such as total nitrogen and water content. Lepidopteran biomass and numbers were correlated with leaf damage in the samples. Leaf-mining, averaging 31 mines per m^2 of leaf area, was significantly higher in the lower canopy. Gall densities approached three galls per m^2 of leaf area. Galled leaves were significantly larger and less heavily grazed. Patterns of herbivory and leaf-mining observed are discussed in light of current information and theories relevant to insect-plant interactions in rain forests.

THERE ARE EXTENSIVE STUDIES ON HERBIVORY UPON RAIN FOREST TREES with regard to forest type and tree species (Coley 1982; Wint 1983; Cooke *et al.* 1984; Dirzo 1984; Lowman 1984, 1985a; Newbery & de Foresta 1985), tree growth strategy (Coley 1982), tree phenology, location and abundance (Lowman 1985a), and tree age (Dirzo 1984, Newbery & de Foresta 1985). However, little is known about the spatial distribution of herbivory within crowns of mature rain forest trees (Lowman 1985a). This is an important topic, since, in rainforest environments, variation in sunlight intensity can alter habitat over a distance of only a few metres. Consequently, sunlight can modify the host-plant substrate and may influence the foraging behaviour and the oviposition patterns of herbivorous insects on a similar scale. The paucity of data about this subject has arisen mainly from logistic problems in canopy access and sampling. Previous studies on rainforest herbivory have focused on the botanical implications of observed patterns. Few authors have recorded the actual chewer load while scoring leaf damage and discussed the implications from an entomological point of view. The present study aimed to assess major determinants of the spatial distribution of herbivory, leaf-mining and gall-forming on an Australian rainforest tree, *Argyrodendron actinophyllum,* and their relation with herbivore abundance.

STUDY SITE

The study was carried out in a stand of complex notophyll vine forest (warm subtropical rain forest) located in the Mount Glorious State Forest (27°19′20″S, 152°44′55″E, altitude 700 m) some 30 km NW of Brisbane, Queensland, Australia. A detailed account of the floristics of the site is found in Young (1985). The canopy reaches 35–40 m on the site, with *Ficus watkinsiana* as an emergent (~45 m). The Mt. Glorious climate can be classified as "slightly seasonal humid," with a summer rainfall regime. Further details about the study site are reported in Basset (1989).

Argyrodendron actinophyllum (Bailey) Edlin, 1935 (Black Booyong) is a tall Sterculiaceae (Malvales), up to 50 m high (Boland *et al.* 1984). This tree represents one of the dominant canopy species of the warm subtropical rain forests in Australia. Distinctive features of this evergreen species include plank buttresses, thick and scaly bark, and palmate leaves of three to nine leaflets with conspicuous domatia. In the Mt. Glorious area, the leaf flush of this species is synchronous among individuals and occurs from October to February (Basset 1989). *Argyrodendron actinophyllum* is a long-lived species

[1] Received 13 July 1990, revision accepted 15 January 1991.

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of intermediate tolerance, often referred to as a late secondary species (Young 1985). Detailed accounts of the phenology and distribution of this tree are reported in Boland *et al.* (1984) and Basset (1989).

METHODS

Canopy access was provided by single rope techniques (Perry 1978) and fifteen trees were climbed on a regular basis. Foliage samples of 0.7 m^2 of leaf area were enclosed with a plastic frame, fogged with CO_2, and the frame was shaken vigorously (further discussed in Basset 1990). Collected arthropods were stored in 70 percent ethanol and sorted to families and morphospecies, which were examined subsequently by various taxonomists. Selected ecological attributes of the foliage sample were measured: height and illumination of the sample, leaf cohorts, leaf damage, epiphyll cover, missing leaflets, *etc.* Leaf sub-samples were harvested for leaf water content, specific leaf weight, total nitrogen, and fibre content analyses (Basset 1989). All the leaves from the sample were measured in order to compute the sample area (16,790 leaves measured). The whole sampling procedure allowed for repetition of sampling within the same canopy, with minimal ecological disturbance.

Leaf cohorts were recognised as follows: "very young leaves" (*i.e.,* reddish colour and measuring less than half of the mature dimensions), "young leaves" (*i.e.,* pale green colour and measuring more than half of the mature dimensions) and "mature leaves" (*i.e.,* fully expanded and pigmented). Subjective assignment of samples was made to three illumination categories: samples in sun most of the time, samples in shade most of the time, and samples in-between these previous illumination levels. Hereafter, the first and second categories are termed **sun** and **shade** samples, but it should be noted that the latter refer to leaves growing in semi-shaded conditions inside tree crowns, rather than to leaves experiencing deep shade conditions in the field layer. The percentage of apparent leaf damage (**ALD**) was scored visually for each leaflet of the sample. The scoring system followed that of Wint (1983) and consisted of the following score classes: **0**: 0 percent, **1**: 0–2.5 percent, **2**: 2.5–5 percent, **3**: 5–15 percent, **4**: 15–30 percent, **5**: 30–45 percent, **6**: 45–60 percent, **7**: 60–75 percent, and **8**: 75–100 percent. The average ALD of the sample was calculated as the average percentage damage per leaflet, obtained in summing the mid-point value of corresponding class scores and dividing this sum by the number of leaflets (Wint 1983). Apparent leaf damage was computed for very young leaves (ALDY1), young leaves (ALDY2), mature leaves (ALDM), and for all leaf cohorts (ALD). Leaf-miner tracks were scored separately, as were galls. The accuracy of this visual assessment was compared on a sample of 0.7 m^2 with reconstruction of the initial shapes of leaflets (with masking tape) and measurements with a leaf area meter (Wint 1983). The error was found to be less than 2 percent (174 leaflets considered). Therefore, it was assumed that no calibration was required for these visual assessments (see Landsberg 1989), probably because the shape of Black Booyong, compound leaves allowed a precise reconstruction of the outline of potentially undamaged leaflets. Visual estimations of ALD have generally been found to be quite reliable (Wint 1983, Cooke *et al.* 1984). An estimation of the leaf biomass removed (**BIOR**) per sample (g dry weight; see discussion of Waller & Jones 1989) was computed by multiplying sample leaf areas removed by specific leaf weights of corresponding leaf cohorts. This estimation was corrected by sample size and expressed per 0.7 m^2 of leaf area. Unless stated otherwise "leaf damage" refers to leaf area removed and "mining density" refers to cumulative (total) mining density, both active and inactive mines considered.

For a given sampling event, 16 samples were taken from each tree. They comprised eight samples from the lower crown (15–25 m; none of the study trees displayed branches lower than 15 m above the ground) and eight samples from the upper crown (25–35 m). In each of these layers, two samples were taken from each of the four possible access points within the tree crown (usually four lines oriented N-S-E-W). A total of 240 such "restricted canopy fogging" samples was obtained from 10 trees during four sampling events in 1987, with four trees being sampled extensively. The overall leaf area sampled represented about 165 m^2. In most cases, sampling was restricted to the inner part of the tree crown, since single rope techniques did not provide ready access to crown periphery and to the top layer of foliage. The highest samples taken were usually 3–4 m below the uppermost leaf layer. In March 1988, the foliage attributes of 800 mature leaves from the uppermost layer of four trees were recorded by climbing to the highest access point and clipping off branches with a pole-pruner of 4 m length. Since leaflet damage distribution was non-normal, even after data transformation, non-parametric statistical tests were used for data analysis. Means are presented with their standard errors throughout the paper.

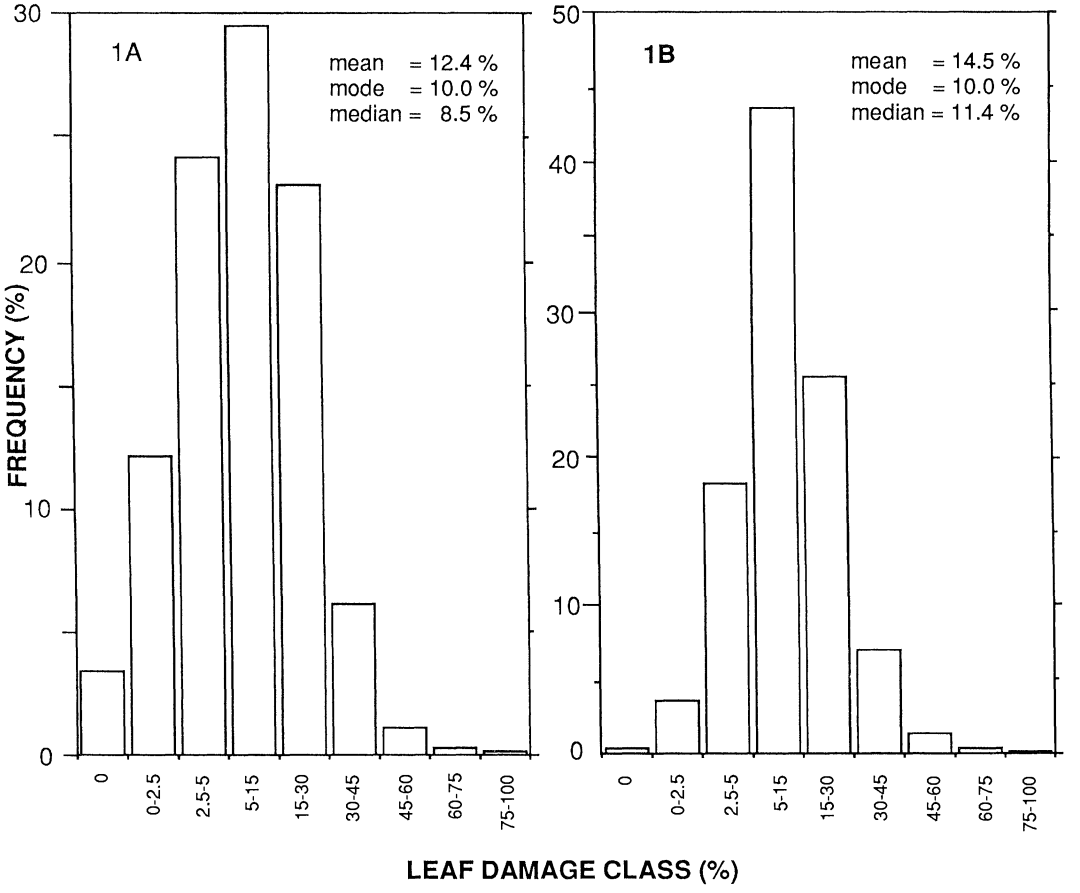

FIGURE 1. Frequency distribution of damage for all leaflets examined (1A, N = 56,459) and for young leaflets only (1B, N = 5182), per ALD scoring class.

RESULTS

OVERALL PATTERNS OF LEAF ATTACK.—Although no records were kept of different grazing types, the loss of leaf area was subjectively attributed primarily to edge grazing and leaf holing by lymantriids, geometrids, chrysomelids, curculionids and scarabeids, which were common on Black Booyong foliage. Skeletonisation was extremely rare. Leaf mining represented only about 5.3 percent of ALD measurements. The frequency distributions of damage for all leaflets and young leaflets examined are presented in Figures 1A and 1B. A test of the overall distribution for the goodness of fit to the Poisson distribution showed that leaflet damage was distributed non-randomly (χ^2 = 7623.2, P < 0.001). Apparent damage to *A. actinophyllum* leaves amounted to about 11 percent and was significantly different among the trees examined (Table 1; values for other trees less extensively sampled are detailed in Basset 1989).

Herbivory for *A. actinophyllum* focused on young leaves, since (a) herbivore populations were restricted to young foliage, which was higher in foliar nitrogen than mature leaves; (b) feeding records of herbivores collected from Black Booyong crowns were limited to the "young leaves" cohort (arguments a and b: Basset 1989); (c) young leaves appeared more heavily grazed than adjacent mature leaves within the samples (ALDY2: 15.89 ± 1.095%; ALDM: 12.32 ± 0.641%; Wilcoxon signed ranks test; P < 0.01, N = 43), despite holes growing faster than expanding leaves (unpubl. data). Leaf damage was furthermore correlated with leaflet abscission (r_s = 0.280, P < 0.001). This suggests strongly that little subsequent damage occurs on mature leaves and that abscission of heavily grazed leaflets is common. This last event may in return

TABLE 1. *Summary of statistics related to herbivory, mines, and galls recorded from four Black Booyong trees sampled extensively.*

Variable[a]	Overall $N = 160$	Lower crown $N = 82$	Upper crown $N = 78$	Mann-Whitney U	Tree 7 $N = 48$	Tree 8 $N = 48$	Tree 9 $N = 32$	Tree 10 $N = 32$	Kruskal-Wallis test
LAT	3486.1	3363.0	3616.0	2818 n.s.	3004.5	3534.3	4393.1	3230.3	36.53***
	(82.3)	(110.5)	(121.4)		(143.6)	(121.2)	(188.9)	(132.9)	
LENG	9.10	9.75	8.43	4545***	9.23	10.54	7.98	7.89	56.49***
	(0.142)	(0.187)	(0.190)		(0.187)	(0.215)	(0.234)	(0.305)	
MISS	31.2	33.7	28.52	3751 n.s.	23.6	18.4	16.2	76.7	56.48***
	(2.61)	(3.45)	(3.97)		(3.02)	(2.56)	(2.99)	(6.69)	
SLWM	100.9	96.2	105.7	1803***	102.7	95.9	112.7	93.4	44.20***
	(1.07)	(1.33)	(1.49)		(1.95)	(1.45)	(2.06)	(1.89)	
ALD	11.22	10.42	12.06	2675 n.s.	13.80	6.46	12.52	13.20	63.72***
	(0.431)	(0.553)	(0.658)		(0.816)	(0.349)	(0.846)	(0.819)	
BIOR	4.64	3.88	5.43	2306**	6.01	2.34	6.01	4.56	56.23***
	(0.248)	(0.291)	(0.388)		(0.494)	(0.150)	(0.582)	(0.464)	
MINE	20.96	24.04	17.71	3808*	19.64	24.62	17.12	21.28	2.51 n.s.
	(1.317)	(2.030)	(1.580)		(2.290)	(2.980)	(2.180)	(2.510)	
GALL	2.05	2.51	1.56	3519 n.s.	2.00	3.58	0.31	1.56	25.03***
	(0.250)	(0.424)	(0.259)		(0.319)	(0.690)	(0.164)	(0.297)	

[a] Variables: LAT = Total leaf area of the sample ($cm^2 \times sample^{-1}$), leaves considered one-sided; LENG = Mean length of the largest leaflet per leaf within the sample (cm); MISS = Total number of missing leaflets per sample (No. $\times$ $sample^{-1}$); SLWM = Mean specific leaf weight of mature leaves (10^{-4} g $\times$ cm^{-2}); ALD = Mean apparent leaf damage per sample, both mature and young leaves considered (%); BIOR = Mean leaf biomass removed per sample (g DW $\times$ $sample^{-1}$); GALL = Total number of galls, active and inactive, recorded per sample (No. $\times$ $sample^{-1}$); MINE = Total number of mines, active and inactive, recorded per sample (No. $\times$ $sample^{-1}$).

TABLE 2. *Herbivory upon leaves from the top layer of Trees 7 to 10.*

Variable	Tree 7	Tree 8	Tree 9	Tree 10	Kruskal-Wallis test
No. of leaves sampled	200	200	200	200	—
LENG	7.2 (0.5)	8.1 (0.6)	7.7 (0.6)	6.4 (0.5)	$P < 0.001$
ALD	11.9 (0.8)	11.3 (0.8)	14.5 (1.0)	13.8 (1.0)	$P < 0.001$

decrease the ALD score of mature leaves to a level apparently lower than that of young leaves. Leaf damage also appeared higher on young leaves than on very young leaves (mean ALDY2 = 15.89 ± 1.095% and ALDY1 = 6.20 ± 0.772%, Wilcoxon test, $P < 0.001$).

An unidentified cecidomyiid species mined young leaves in spring, while several species of unidentified Lepidoptera, including some tineids, mined the mature foliage later in the season. Cumulative mining densities on *A. actinophyllum* foliage averaged 30.6 mines per m^2 of foliage or about 30–37 mines per 100 leaves and were not significantly different between trees (double-sided leaf area, Table 1). Two types of leaf galls, whose primary gall-makers are unknown, grew on mature foliage during winter. Twig and bud galls, which were relatively scarce and probably initiated by several species of Megastiminae (Hymenoptera: Torymidae), were not included in the present analysis. More variance in galling density was expressed among the trees than within the trees (Table 1).

VARIATION OF LEAF ATTACK WITHIN TREES.—Herbivory was slightly higher in the upper canopy than at lower levels, but not significantly so (Table 1, $P = 0.07$). Although sample size was small, no extensive differences were detected between leaf damage recorded from the uppermost leaf layer (Table 2) and that recorded from the lower crown (Mann-Whitney $U = 62.9$, $z = -1.59$). Leaf damage differed significantly among sample illumination levels, but not among sample compass orientations (Table 3) and was patchily distributed within the crown, with sharp differences among samples separated by only a few branches. Leaf damage on mature leaves (excluding samples with young foliage) was higher in the sun than in the shade (Mann-Whitney $U = 58$, $P < 0.001$). Young foliage was significantly more abundant in sun samples than in shade samples and sun leaves were smaller and heavier than shade leaves (Table 3). Leaf biomass removed amounted to 6.7 g dry weight per m^2 of foliage, was significantly higher in the upper canopy and in sun samples, and differed significantly among trees examined (Tables 1 and 3).

Mining densities were significantly higher in lower canopy (Table 1) and in shade samples (Table 3). Mines were distributed non-randomly and mined leaves were significantly larger, included more leaflets, and were less heavily grazed than unmined leaves (Table 4). Within-leaf distribution of mines

TABLE 3. *Leaf characteristics and herbivory with regard to the illumination and compass orientation of the samples in four trees sampled extensively.*

	Shade $N = 68$	In-betw. $N = 80$	Sun $N = 12$	Kruskal-Wallis test	North $N = 40$	South $N = 39$	East $N = 37$	West $N = 44$	Kruskal-Wallis test
LENG	10.02 (0.20)	8.44 (0.18)	8.34 (0.34)	27.58***	8.77 (0.22)	9.81 (0.32)	9.45 (0.32)	8.48 (0.24)	7.85**
SLWM	90.6 (2.2)	104.1 (1.9)	112.5 (3.8)	39.80***	104.4 (2.2)	96.4 (3.5)	95.1 (4.1)	99.9 (1.6)	0.58 n.s.
ALD	8.97 (0.51)	12.01 (0.54)	18.65 (2.2)	27.30***	10.72 (0.81)	10.47 (1.14)	10.47 (1.14)	12.67 (0.71)	2.42 n.s.
BIOR	3.12 (0.22)	5.20 (0.32)	9.48 (1.34)	36.99***	4.28 (0.52)	4.46 (0.32)	4.33 (0.48)	5.37 (0.59)	2.99 n.s.
MINE	27.6 (2.27)	16.2 (1.54)	15.2 (1.30)	17.31***	18.9 (2.19)	20.4 (2.61)	23.5 (3.36)	20.9 (2.27)	1.09 n.s.
GALL	2.91 (0.50)	1.15 (0.19)	3.16 (1.0)	8.08*	2.64 (0.60)	1.59 (0.55)	1.50 (0.35)	2.41 (0.50)	5.05 n.s.

TABLE 4. *Summary of data relevant to mine distribution.*

A Number of leaves with N mines

N	0	1	2	3	4	5	6	7	8	9
Number of leaves	9080	1079	880	624	376	140	120	56	16	63

χ^2 test for random distribution = 6781.8***

B	Unmined leaves (N = 9080)	Mined leaves (N = 3354)	Mann-Whitney test
Length	8.01 ± 0.03 cm	10.49 ± 0.07 cm	$P < 0.001$
No. leaflets	5.55 ± 0.02	6.03 ± 0.04	$P < 0.001$
No. missing leaflets	0.20 ± 0.067	0.31 ± 0.018	n.s.
ALD	13.54 ± 0.118%	8.81 ± 0.180%	$P < 0.001$

C Location of mine on Nth leaflet

N	1st	2nd	3rd	4th	5th	6th	7th	8th	9th
No. leaves (a)	704	725	658	513	355	190	125	74	10
No. leaflets censused (b)	1886	1846	1731	1558	1315	1020	718	424	181
Ratio a/b × 100	37	39	38	33	27	17	17	17	6

χ^2 test on the five first leaflets = 121.9***

was not random on the first five leaflets, and was slightly higher on mid-leaflets (*i.e.,* second and third leaflets), which are usually larger in the palmate leaf of *A. actinophyllum* (Table 4, the first five leaflets were retained as a leaf includes, on average, 5.3 leaflets). Galled leaves were distributed non-randomly and were significantly larger and less heavily grazed (Table 5).

HERBIVORY IN RELATION TO LEAF TRAITS AND TO HERBIVORE ABUNDANCE.—ALD was positively correlated with specific leaf weight and fibre content, and negatively correlated with the size, nitrogen, and water content of mature leaves (Table 6). Leaf biomass was also negatively correlated with the size, nitrogen, and water content of leaves and was positively correlated with specific leaf weight and fibre content (Table 6). Leaf damage on young leaves (ALDY2) was not correlated with foliar nitrogen of young leaves ($r_s = -0.09$, n.s.). Neither item was correlated with translocation effects (variable TRANS, leaf nitrogen of young leaves minus the corresponding value for mature leaves within the sample; $r_s = -0.04$, n.s.) nor with leaf water ($r_s = 0.11$, n.s.). Herbivory on young foliage was best correlated with the length of young leaves ($r_s = -0.389$, $P < 0.05$) and with a variable expressed as the ratio of specific leaf weight of young leaves to young foliage available in the four closest adjacent samples (*i.e.,* a measure of the isolation of sunny patches of young foliage; $r_s = 0.611$, $P < 0.001$). This suggests that isolated, abundant, and sunny patches of young foliage may experience higher damage and that herbivore feeding bouts may be localised and/or quite distant from each other. Since the number and the area of young leaves within the sample were posi-

TABLE 5. *Summary of data relevant to gall distribution.*

A Number of leaves with N galls:

N	0	1	2	3	4
No. leaves	12,106	200	90	30	8

χ^2 test for random distribution = 997.8***

B	Ungalled leaves (N = 12,106)	Galled leaves (N = 328)	Mann-Whitney test
Length	8.41 ± 0.031 cm	10.32 ± 0.210 cm	$P < 0.001$
No. leaflets	5.64 ± 0.017	5.42 ± 0.111	n.s.
No. missing leaflets	0.22 ± 0.07	0.43 ± 0.055	$P < 0.05$
ALD	12.74 ± 0.105%	10.20 ± 0.616%	$P < 0.001$

TABLE 6. *Selected values from the correlation matrix (Spearman rank correlation coefficient) established between the variables ALD, BIOR, MINE, GALL and selected variables recorded from the samples.*

	BIOR	MINE	GALL	LENG	MPC[a]	LAY2	NITM	SLWM	LWCM	ADFM
ALD	0.92	n.s.	n.s.	−0.58	n.s.	n.s.	−0.39	0.39	−0.37	0.22
BIOR	—	n.s.	n.s.	−0.65	n.s.	n.s.	−0.32	0.59	−0.35	0.28
MINE	—	—	n.s.	n.s.	0.48	−0.41	−0.19	n.s.	n.s.	n.s.
GALL	—	—	—	n.s.	0.20	−0.40	n.s.	n.s.	n.s.	n.s.

[a] Variables not defined in Table 1: MPC = Mean epiphyll percentage cover per sample, all leaves considered (%); LAY2 = Leaf area of young leaves ($cm^2 \times sample^{-1}$); NITM = Mean foliar nitrogen of mature leaves ($mg \times g^{-1}$ DW); LWCM = Mean leaf water content of mature leaves (%FW); ADFM = Mean percentage fiber of mature leaves (%DW); $N = 160$, exception made of correlations involving LAY2 ($N = 43$); Correlations indicated are all significant, at least with $P < 0.05$.

tively correlated with the magnitude of translocation within the sample ($r_s = 0.589$ and $r_s = 0.608$, respectively, $P < 0.001$), the negative correlation in mature samples between leaf damage (ALDM) and nitrogen was not surprising ($r_s = -0.431$, $P < 0.001$, $N = 111$): portions of the crown in which leaf production is higher have their nitrogen "drained out" from mature leaves for vegetative growth.

Mine abundance was negatively correlated with nitrogen and positively correlated with epiphyll percentage cover of mature leaves (Table 6). However, these measurements refer mostly to inactive mines and nothing can be stated about the initiation of active mines and its possible correlation with leaf nutrients. Leaf-mining was positively correlated with the leaf area of larger leaves within the sample, but not with leaf length. A positive correlation existed between leaf damage on young leaves and caterpillar abundance and biomass ($r_s = 0.322$ and 0.328, respectively, $P < 0.05$). Furthermore, mean leaf damage on young leaves was significantly higher for samples including caterpillars than for samples devoiding these insects (18.5 ± 2.22% and 11.7 ±1.42%, respectively, Mann-Whitney $U = 150.0$, $P < 0.05$). This strongly suggests that most leaf damage is caused by caterpillars. Biomass and numbers of other herbivore groups were not correlated with leaf damage. Psyllid abundance was negatively correlated with leaf damage on young leaves ($r_s = -0.365$, $P < 0.05$). Leaf damage within mature foliage samples was positively correlated with the abundance of all arthropods combined ($r_s = 0.224$, $P < 0.05$). Probably these observations are related to higher leaf damage in sun samples, where most groups were more abundant (Basset 1989).

DISCUSSION

HERBIVORE DAMAGE ON BLACK BOOYONG LEAVES.— Since few leaflets remained intact on the Black Booyong trees (<4%), the distribution of leaf damage was distinct from that reported for other trees (Dirzo 1984, Landsberg 1989). Scoring leaf damage on evergreen leaves may be misleading: small necrotic areas may be caused by factors independent of insect herbivory (*e.g.*, fungal diseases, pronounced action of weather in rainforest environments, *etc.*) and may accumulate with age. Very few leaflets were extensively grazed: damage higher than 30 percent was recorded from only 7.6 percent of the cases (however, leaflets entirely eaten may be relatively common: Lowman 1984). This abrupt decline in leaf area eaten suggests that these leaves are not nutritionally very rewarding and that herbivores, particularly generalists, may subsequently switch to other leaflets or consume suitable leaflets completely. Another explanation may pertain more specifically to leaf chemical defences. Mucilage cells and canals, which are abundant in Black Booyong leaves (pers. obs.), may "gum up" generalist chewers or discharge digestibility reducers, which may prevent an extensive consumption of foliage.

The discrepancies between long-term monitoring of insect damage and discrete measurements of ALD, which underestimates leaves entirely eaten and therefore underestimates insect grazing, may be important (Lowman 1984, 1985a, b). Grazing of entire *A. actinophyllum* leaves appears uncommon. The leaf petiole is quite long (up to 10 cm), thick (4–5 mm in diameter) and even when young, hard to cut and remove. When leaves are extensively eaten, the petiole and even the remaining petiolules are still conspicuous signs of the fate of the leaf, which can be scored accordingly. In contrast, missing leaflets are commonplace and represent an average loss of 305 cm^2 per sample. Therefore, the total apparent loss of leaf area (as represented by ALD, missing leaflets, and mining tracks) can amount to 18.9 percent for an average sample. However, as more samples were obtained at the peak time of

leaf production, leaflet abscission may have been promoted mostly by translocation rather than by herbivore damage, and the overall apparent leaf damage should amount to between 11.2 percent (ALD, Table 1) and 18.9 percent. Estimates of apparent leaf damage on mature leaves may not represent actual leaf consumption by herbivores, because they may be biased after herbivore damage by the subsequent hole expansion during leaf growth (Landsberg 1989). However, because herbivory on Black Booyong was confined to the "young leaves" cohort, and holes measured on mature leaves were not proportional to leaf growth, actual leaf consumption by herbivores can be more securely estimated within the range of leaf area removed from young leaves: 16 percent without counting missing leaflets and 23 percent counting leaflets entirely eaten and loss by abscission. Leaflet abscission on "very young leaves" was a common event, which occurred before most of herbivore damage. Therefore the lower bound of the previous estimation (16%) reflects probably an acceptable figure for leaf consumption by Black Booyong herbivores.

The ALD recorded for *A. actinophyllum* thus appears to be within the upper range of the mean values reported from other rainforest sites investigated with a similar methodology: 12.7 percent and 12.5–13.7 percent in Panama and Papua New Guinea, respectively (Wint 1983); 8.5 percent in Mexico (Dirzo 1984); 5.5 percent in French Guiana (Newbery & de Foresta 1985). Cooke *et al.* (1984) similarly reported mean ALDs of 6.2 and 13.4 percent for two rainforest tree species from Sarawak. Lowman (1984, 1985a) studied five Australian rainforest species at several sites and reported a general ALD of 8.3 percent (corresponding to a long-term assessment of 14.6 %) for Australian subtropical rain forests and long-term values in particular ranging from 8.5 percent to 48 percent for *Argyrodendron trifoliolatum.* Overall leaf damage may be relatively high on Black Booyong for at least three reasons. Firstly, chemical defences in young leaves may be lowered to facilitate the growth strategy of this late secondary species (Coley 1982). Secondly, foliicolous predators were relatively inefficient in controlling herbivores during the restricted leaf production period of this tree. Spiders avoided young foliage, and arboreal ants were scarce (Basset 1989). Thirdly, leaf damage expressed as mean damage per leaf within samples may overestimate grazing values, particularly if damage distribution is non-normal (Landsberg 1989).

Leaf-mining values for Black Booyong fall into the range of cumulative mining densities reported for temperate trees (*Fagus*: 80 mines/100 leaves: Nielsen & Ejlersen 1977, *Quercus*: 2–18 mines/100 leaves: Faeth *et al.* 1981). However, estimates of cumulative densities on mature foliage of evergreen rainforest trees may overestimate mining rates, because of the long lifespan of rainforest leaves. The densities of active mines on *A. actinophyllum* were far lower, as exemplified by active cecidomyiid mines on young leaves: about 3.9 mines per m^2 of young foliage or 4 mines per 100 young leaves. This suggests that mining on young foliage is restricted and that most of the mining activity occurs after the two months following leaf emergence.

STRATIFICATION OF HERBIVORE DAMAGE AND RELATION TO ILLUMINATION.—Apparent leaf damage was not significantly higher in the upper canopy than at lower levels, but this comparison was significant when data were expressed in leaf biomass removed. Lowman (1985a) reported that in Australian subtropical rain forests, leaves close to the ground level are more heavily grazed. Her definitions of **lower** (0–3 m) and **upper** canopy (>10 m) were quite different from those of the present study and her leaf-monitoring stations in the upper canopy were ≤25 m (Lowman 1985a). Herbivores foraging within mature Black Booyong trees were unlikely to encounter leaves growing in deep shade conditions, such as the leaves sampled by Lowman (1985a) in the field layer. Therefore, the results of the present study are not conflicting regarding the stratification of leaf damage. Effectively, grazing may be more intense near ground level, as some generalist herbivores may specialise on feeding within the shrub layer, particularly on saplings. This would partly explain the occurrence of herbivorous taxa in control interception traps set up at ground level at the Mt. Glorious study site (Basset 1989). Since young leaves are probably rarer (per unit volume of foliage) in the shrub layer than in the upper canopy, herbivores would tend to aggregate on young shrub-layer leaves according to the resource concentration hypothesis (Root 1973). This would result in a higher ALD within the shrub layer. Furthermore, Frankie *et al.* (1974) documented that continuous leafing is more widespread among understory rainforest trees than among overstory trees. This factor may further contribute to increased leaf damage near ground level.

There is great conflict in reports about the palatability of shade and sun leaves to herbivores in the entomological literature. Shade leaves were found in some instances to be more palatable than sun leaves and therefore more heavily grazed by folivores (Maiorana 1981, Lowman 1985a). However, this

view has been refuted or questioned by several authors (Lincoln & Mooney 1984, Claridge 1986, Harrison 1987, Louda *et al.* 1987). Usually sun leaves are higher in soluble nitrogen (Mooney & Gulmon 1982), and this may explain their higher palatability, which compensates for their lower water content and higher toughness and phenol levels (Claridge 1986, Harrison 1987). Young foliage of Black Booyong was not confined to upper levels of the canopy but was distributed patchily in the crown according to illumination levels. Yet samples consisting of mature leaves were more damaged in sun than in shade. Total nitrogen and fibre, expressed per unit leaf area were significantly higher in sun leaves than in shade leaves (unpubl. data), and this comparison may be even more marked for soluble nitrogen. In fact, resource concentration may also account for the relative palatability of sun and shade leaves in rain forests: the grazing pressure may depend on the relative density of sun and shade young leaves.

Mining on Black Booyong leaves appeared to be higher on more shaded and larger leaves. Generally mining densities are reported to be higher on shaded leaves, although shading effects may vary among miner species (Nielsen & Ejlersen 1977, Faeth *et al.* 1981). Several studies have shown that leaf size may be important in the selection of suitable leaves by miners, providing that mine size is relatively large (Faeth 1985). In the present study, leaf size seems to be an important factor for miners. This may be influenced further by leaflet abscission and interference with chewers (Nielsen 1978, Faeth 1985). If these observations are verified, it may explain why oviposition by miners on sun leaves in the upper crown of *A. actinophyllum* is not favoured. Galls, despite being more abundant in larger leaves, were also rather numerous in sun samples, thus gall distribution appeared to be distinct from that of mines. Probably galls were physically better defended against chewing interference than were mines (let aside the possible influence of gall chemical composition) particularly because gall-makers oviposited within the main leaf nervure, which was usually avoided by chewers.

PREDICTING HERBIVORE DAMAGE.—Leaf damage on Black Booyong appeared to be more dependent on the location of isolated, abundant, and sunny patches of young foliage than on local differences in foliar nutrient characteristics, such as total nitrogen and water content. However, chemical defences (other than fibre) and soluble nitrogen may also influence the distribution of leaf damage. Herbivore microclimate requirements and predator avoidance strategies (particularly those of avoiding avian predators) may contribute to the observed pattern. Leaf size and biomass are important for chewers such as caterpillars, as they affect apparency to predators, and lead to reduction of movement costs when a locally abundant and suitable source of food is located (Schultz 1983). Leaf damage differed significantly among the study trees, was patchily distributed, and appeared to result from a set of complexly interrelated variables including leaf production, illumination, and foliage denseness. However, with such a restricted number of trees examined, and in the absence of any precise information about illumination levels within these trees, any interpretation remains speculative.

Lepidoptera was the only herbivore group whose biomass and numbers were correlated with leaf damage on Black Booyong. Furthermore, there appeared to be no relationship between average leaf damage or average leaf biomass removed per tree and the actual chewer load (Basset 1989). These observations suggest that patterns of overall grazing (as recorded by ALD measurements) are largely dominated by only a few individuals, which ingest considerable amounts of photosynthetic leaf tissue (*i.e.,* caterpillars). Small folivore populations can cause disproportionately large foliage loss by feeding on vegetative buds or unexpanded leaves. However, ALD measurements, so often used as an index of herbivore abundance in the entomological literature, refer only to a restricted portion of the herbivore community, usually the lepidopteran community. Indeed, the spatial distribution of leaf damage as a whole, although relatively easy to assess, is of limited value in the study of herbivore distribution, unless types of grazing damage pertaining to the insects responsible can be accurately and separately recorded.

Young leaves suffered proportionally higher damage than very young leaves and this was consistent with the field distribution and feeding behavior of herbivores (Basset 1989). This suggests an optimum time for grazing, after the first two weeks of expansion. The emerging leaves of *A. actinophyllum* are protected with a sticky coating that may deter herbivore feeding. This mechanical (and possibly chemical) protection may replace protection with alkaloids (absent in this species: Webb 1952) or with phenols and tannins, which usually accumulate with age (Lowman & Box 1983). The negative correlation observed between psyllid abundance and leaf damage on young leaves is probably related to the preference of these insects for newly

emerged leaves which are avoided by other herbivores. Journet (1980) reported that the second best abundance predictor, after leaf age, of psyllids *Glycaspis* spp. on their eucalypt host was the probability of foliage escape from herbivory.

In conclusion, sunlight appears to be a factor of primary importance for the spatial distribution of herbivory within the crowns of the rainforest tree *A. actinophyllum*. Illumination levels deeply affect both leaf morphology and the local magnitude of leaf production, to which chewers such as caterpillars are particularly sensitive. Leaf chemical defences, which influence herbivore attack, are also presumably altered by sunlight, but such investigations were beyond the scope of this study.

ACKNOWLEDGMENTS

I am deeply indebted to Prof. R. L. Kitching and Dr. A. H. Arthington for their support during the study. N. D. Springate checked the manuscript, which benefited from valuable comments by Drs. M. D. Lowman, D. Burckhardt, I. Löbl, and an anonymous reviewer. The Queensland Department of Forestry allowed me to carry out the research in the Mt. Glorious State Forest. The research was funded by a Griffith University Postgraduate Research Scholarship.

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