

Influence of leaf traits on the spatial distribution of arboreal arthropods within an overstorey rainforest tree

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Abstract. 1. Several attributes of foliage were measured from the Australian rainforest tree *Argyrodendron actinophyllum* Edlin (Sterculiaceae). These were related to estimates of abundance per leaf area of the most common arthropod guilds and families sampled with restricted canopy fogging.

2. When all these arthropod groups were considered, much of the overall variance in arthropod spatial distribution could be attributed to leaf age characteristics, arthropod aggregation patterns, arthropod activity and distance to tree trunk.

3. The fraction of variance which could be specifically explained by foliage attributes such as nitrogen-, water- and fibre-content, specific leaf weight, and epiphyll load was small for most arthropod groups (usually <30%). However, an index of food quality explained a higher proportion of variance (50%) in the abundance of phloem-feeders. Leaf size and foliage compactness did not influence significantly the abundance of any arthropod group.

4. Most herbivores were more abundant on young foliage than on mature leaves. With the exception of Corylophidae and Chrysomelidae, which were more abundant in the lower and upper canopy respectively, arthropod stratification was not conspicuous within the inner core of tree crowns.

5. The results firstly emphasize the distribution of young foliage as a key factor affecting the abundance of many herbivores and, secondly, the importance of the local illumination regime for host leaf production and its indirect effects on the spatial distribution of arboreal arthropods.

Key words. Arboreal arthropods, *Argyrodendron*, nitrogen, rain forest, stratification, spatial distribution.

Introduction

Studying and predicting the spatial distribution of phytophagous insects is one of the major concerns in forest entomology. Research into insect population dynamics requires a correct assessment of insect spatial distribution, and estimation of absolute population size often involves stratified or proportionate sampling of the insect population within tree crowns (e.g. Morris, 1955). The various biochemical features, microhabitats and microclimates provided by rainforest trees render them particularly interesting for the study of spatial distribution and aggregation in herbivorous insects, although access and sampling within the rainforest canopy are difficult and limited.

However, the development of single rope techniques in rainforest environments (Perry, 1978) has produced interesting sampling opportunities for tropical entomologists, which, at present, remain under-exploited (Lowman, 1985; Basset, 1988, 1989, 1990). Hence, little is known about arthropod spatial distribution in the rainforest canopy and the published information concerns primarily herbivore distribution in the shrub layer (e.g. Harrison, 1987; Ernest, 1989; Macedo & Langeheim, 1989) and insect flight-activity in the canopy (e.g. Wolda, 1979; Sutton, 1983, 1989). Insect light-trapping in various rain forests by Sutton (1983) showed that flight activity was higher in the upper canopy than below and that local topography accounted for the magnitude of the observed differences in stratification. Patterns of spatial distribution of arthropods are likely to depend on several parameters, which in turn may induce arthropod stratification within rainforest trees. For example, (a) since the nutrient avail-

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ability of evergreen rainforest foliage is usually low and nitrogen is a limiting factor for herbivores (e.g. Mattson, 1980), the micro-distribution and abundance of nitrogen-rich young foliage may be a key determinant of herbivore distribution; (b) host resistance to herbivory, mediated by host maturation processes, can produce nonoverlapping herbivore distributions within tree crowns (Kearsley & Whitham, 1989); (c) since predation pressure is apparently high in rainforest environments (Elton, 1973), foliage compactness may represent an important protection for herbivores from avian and arthropod predators (e.g. Lawton, 1983); (d) illumination patterns *per se* may also be crucial, since they can influence activity and subsequent oviposition behaviour of herbivores (Moore *et al.*, 1988).

This contribution examines the results of a field study which tested the prediction that arthropod distribution within an overstorey rainforest tree was influenced primarily by leaf traits. Arthropod abundance and foliage characteristics were estimated using a sampling method which enabled the relationship between arthropods and foliage inside the inner core of tree crowns to be evaluated statistically. As general patterns in arthropod distribution were looked for, rather than specific species-distribution, the analyses emphasized how all individuals belonging to particular arthropod guilds and families were distributed on the foliage.

Material and Methods

Study site, host-tree and arthropod sampling. The study site was situated in a stand of warm subtropical rain forest (complex notophyll vine forest) at Mt Glorious, near Brisbane, Queensland, Australia (27°19'S, 152°45'E, 700 m). Young (1985) provides detailed floristic data from the study area. *Argyrodendron actinophyllum* Edlin (Sterculiaceae) ('Black Booyong') is an evergreen canopy tree reaching up to 50 m in height, which is characterized by a scaly bark, dense foliage and palmate leaves with domatia. Synchronous flowering usually occurs in April–May and leaf flush in October–January (Basset, 1989). Leaves are retained for at least 3 years.

Canopy access was provided by single rope techniques (Perry, 1978). With the aid of this method, 0.7 m² of foliage were surrounded in a plastic enclosure. Then, carbon dioxide was released into the enclosure at a constant pressure of 1.055 bars for 20 min and the anaesthetized arthropods were subsequently transferred into 70% ethanol ('restricted canopy fogging'). Limitations and discussion of methods, as well as precise sampling protocol are detailed in Basset (1990). Briefly, eighty such samples were collected in various parts of the crowns of ten mature trees during January–February 1987 (trees 1–10). This pilot study led to the design of a sampling programme using four trees (trees 7–10), sampled during three other sampling events: April–May 1987, November–December 1987 and January–February 1988 (160 samples, sampling events 1–3). During a sampling event, sixteen samples were performed within each tree. They consisted of eight

samples from the lower crown (15–25 m) and eight samples from the upper crown (25–35 m), taken equally from each of the four quadrants within the crown (N, S, E and W). Access and sampling was in most cases restricted to the inner core of tree crowns. The specimens collected were sorted to family and morphospecies and then assigned to arboreal guilds according to their trophic requirements (see Basset, 1991a). Arthropod material was deposited at the Queensland Museum, Brisbane, and its taxonomic composition is discussed elsewhere (Basset, 1991b).

Measurement of foliage attributes and statistical analyses. After fogging, selected ecological descriptors of the foliage were surveyed. All the leaves from the sample were measured to compute total sample area using regression curves (leaves considered one-sided). Then, leaf sub-samples were harvested for leaf water content, specific weight, total nitrogen and fibre analyses (oven-drying, Kjeldahl and acid detergent fibre standard procedures respectively). Leaf categories were discriminated on the basis of both leaf cohort and leaf size and each fogging sample was characterized by twenty-six variables (Table 1). The whole sampling procedure allowed repetition of sampling upon the same study trees, with minimal ecological disturbance.

A small increase in sample size had only a marginal influence on total number of arthropods collected. Consequently, estimates of arthropod abundance were not corrected for this factor. Ordination techniques represent a powerful means of quantifying much of the variance expressed by samples-by-taxa matrices, particularly when taxa abundance is low (Legendre & Legendre, 1984), as in the present case. Such techniques usually investigate relations between samples and taxa, not between sample attributes and taxa. A particular ordination, involving a two-step computation and termed hybrid ordination, enables the latter analysis and was performed as follows (Gauch, 1982). Firstly, a detrended correspondence analysis (DCA) was computed on a samples-by-arthropod group matrix of the 160 fogging samples, utilizing the abundance of the forty-five most common arthropod groups (various arboreal guilds, orders and families). Then, the sample ordination scores were used as weights for a weighted averages ordination of the samples-by-foliage attributes in order to obtain ordination scores for the attributes (Gauch, 1982).

In an attempt to quantify more specifically the amount of arthropod spatial variance expressed by the leaf attributes, four new uncorrelated variables were defined in order to perform stepwise multiple regression analyses in avoiding multicollinearity problems. These variables included: an index of food quality (FQI), an index of arthropod activity (ACTI), an index of the age of mature foliage (OLDF) and a climatic index (CLIM). Their choice was guided by the hybrid ordination and by Pearson's correlation coefficients computed between taxa and foliage attributes. The new variables were described by models of additive scores. Each score represented a selected foliage attribute divided by its mean value. The relative importance of the scores within the new variable was weighted

Table 1. Foliage attributes recorded within the samples, their unit values and the corresponding coding variable adopted in the text.

Air temperature recorded (°C)
Illumination of the sample (shaded, intermediate, isolated)
Compass orientation of the sample (N-S-E-W)
Branch axis on which the sample was taken (dimensionless) (AXIS)
Mean compactness of the sample (point quadrat methods: ten handlings of a stick within the sample) (mean no. contacts per sample)
Total leaf area of the sample (cm ²) (LAT)
Leaf area of very small, small, medium-sized and large leaves (cm ²)
Leaf area of very young, young and mature leaves (cm ²) (LAY1, LAY2, LAMT)
Mean length of the largest leaflet per leaf (cm) (LENG)
Total number of missing leaflets per sample (No./sample) (MISS)
Mean apparent leaf damage per sample (%) (ALD)
Mean percentage cover of leaf epiphylls per sample (%) (MPC)
Total number of galls and mines (active and inactive) recorded per sample (No./sample) (GALL, MINE)
Mean leaf water content of young leaves and mature leaves (% FW) (LWCY, LWCM)
Mean specific leaf weight of young and mature leaves (10 ⁻⁴ g/cm ²) (SLWY, SLWM)
Mean foliar nitrogen of young and mature leaves (mg/g DW) (NITY, NITM)
Mean % fibre of young and mature leaves (% DW)

by an exponential equal to the correlation coefficient between the foliage attribute and an indicator taxon. This procedure emphasized the importance of certain foliage attributes, particularly when their measurements were higher than their average values (see mathematical expression of new variables in Table 3 in the result section; for more details refer to Basset, 1989). Stepwise regressions were computed with the usual default value of alpha-to-enter = 0.15 (Bendel & Alfifi, 1977) but more conservative models were computed with alpha = 0.05.

Results

Relations among foliage attributes

The measurements of foliage attributes are detailed in Table 2. Other sample attributes are further discussed and analysed by principal coordinates analysis elsewhere (Basset, 1989). The sum of this information suggests that the lower level of *A. actinophyllum* crowns is characterized by higher leaf area, higher epiphyll load and increased leaf mine densities. In contrast, the upper crown exhibits higher air temperatures, higher branch area within the sample, more small leaves, increased specific leaf weight of mature leaves and increased nitrogen content of young leaves. Furthermore, the occurrence of young foliage was more influenced by local illumination than by height alone.

The abundance of young leaves and the nitrogen content of both young and mature foliage differed between trees. Tree mean leaf production at sampling events 2 and 3 could be ranked as follows: tree 10 (30% of young leaves) > tree 9 (20%) > tree 7 (7.5%) > tree 8 (2.5%). This tree ranking was identical for young foliage area sampled on these trees, for foliar nitrogen of young leaves within these trees and was inversely ordered for foliar nitrogen of mature leaves. These observations and, particularly, the sharp increase in missing leaflets and decrease in nitrogen of mature leaves within tree 10 suggest a relation with

translocation effects (redistribution of photosynthate to young leaves and abscission: Pate, 1980; see further data and discussion in Basset, 1991c). Several other foliage attributes were statistically different between trees (Table 2) and most of these differences were related to the general illumination of the study trees and their crown openness.

Relations between the foliage attributes and the fauna

Plots of the hybrid ordination in the four-dimensional space computed by the DCA are presented in Fig. 1, in which, for sake of clarity, some taxa are omitted. The first axis, which explained 54.0% of the variance in arthropod abundance among the samples, was interpreted as a gradient of foliage age and its suitability for arboreal arthropods. The scores of the samples on this axis were best correlated with the variables NITY, LWCY, SLWY, LAY2, MPC and GALL ($r = 0.741, 0.671, 0.607, 0.603, -0.266$ and -0.209 respectively, $P < 0.01$). Arthropods were segregated along this axis according to their feeding habits. Meristem-feeders, such as psyllid nymphs, were restricted to young foliage. Phloem-feeders and chewers (e.g. Cicadellidae, Chrysomelidae, etc.) preferred young foliage but were sometimes abundant on mature foliage. Mesophyll-feeders (Thysanoptera), parasitoids (Aphelinidae), predators (Araneae and others), wood-eaters (most Curculionidae), fungal-feeders (Corylophidae) and tourists (most of Nematocera) did not exhibit such a strong attraction for young leaves. On the other hand, scavengers (Blattodea) and epiphyte grazers (Psocoptera) were mainly restricted to older foliage. The uncertain group was associated with the developing foliage, as most immatures of Thysanoptera and Heteroptera were assigned to this class. Spiders showed clear preferences for mature foliage.

The second axis of the ordination explained 25.4% of the variance. The scores of the samples on this axis were best correlated with the variable NITY ($r = 0.357$,

Table 2. Mean (SE) of selected foliage attributes recorded during sampling events 1, 2 and 3. Variables and their units as in Table 1.

Variable	Overall (<i>n</i> = 160)	Lower crown (<i>n</i> = 82)	Upper crown (<i>n</i> = 78)	Sign. ⁽¹⁾	Tree 7 (<i>n</i> = 48)	Tree 8 (<i>n</i> = 48)	Tree 9 (<i>n</i> = 32)	Tree 10 (<i>n</i> = 32)	Sign. ⁽²⁾
LAT	3486.1 (82.3)	3363.0 (110.5)	3616.0 (121.4)	n.s.	3004.5 (143.6)	3534.3 (121.2)	4393.1 (188.9)	3230.3 (132.9)	***
LAY2 ⁽³⁾	294.1 (64.6)	391.6 (107.0)	191.6 (69.0)	n.s.	40.4 (21.8)	5.5 (3.4)	516.1 (164.9)	885.5 (242.2)	***
LENG	9.10 (0.142)	9.75 (0.187)	8.43 (0.190)	***	9.23 (0.187)	10.54 (0.215)	7.98 (0.234)	7.89 (0.305)	***
MPC	11.33 (0.592)	13.80 (1.023)	8.74 (0.397)	***	12.84 (1.085)	13.68 (1.434)	9.20 (0.526)	7.69 (0.640)	***
ALD	11.22 (0.431)	10.42 (0.553)	12.06 (0.658)	n.s.	13.80 (0.816)	6.46 (0.349)	12.52 (0.846)	13.20 (0.819)	***
GALL	2.05 (0.250)	2.51 (0.424)	1.56 (0.259)	n.s.	2.00 (0.319)	3.58 (0.690)	0.31 (0.164)	1.56 (0.297)	***
MINE	20.96 (1.317)	24.04 (2.030)	17.71 (1.580)	*	19.64 (2.290)	24.62 (2.980)	17.12 (2.18)	21.28 (2.510)	n.s.
LWCM	52.88 (0.231)	52.83 (0.331)	52.93 (0.326)	n.s.	51.64 (0.373)	55.18 (0.394)	51.64 (0.344)	52.48 (0.433)	***
LWCY ⁽³⁾	65.26 (0.636)	65.14 (0.780)	65.47 (1.138)	n.s.	60.75 (0.350)	65.65 (0.250)	64.11 (0.870)	66.30 (0.910)	n.s.
SLWM	100.9 (1.07)	96.2 (1.33)	105.7 (1.49)	***	102.7 (1.95)	95.91 (1.45)	112.7 (2.06)	93.4 (1.89)	***
SLWY ⁽³⁾	67.5 (2.34)	66.3 (2.63)	69.6 (4.61)	n.s.	77.0 (2.50)	72.1 (1.80)	77.6 (3.23)	60.7 (2.81)	**
NITM	16.19 (0.157)	16.05 (0.267)	16.33 (0.163)	n.s.	16.25 (0.182)	17.20 (0.229)	15.84 (0.254)	14.80 (0.544)	***
NITY ⁽³⁾	18.01 (0.741)	16.54 (0.847)	20.05 (1.183)	*	16.30 (0.100)	13.65 (0.950)	16.69 (0.640)	19.48 (1.190)	n.s.

⁽¹⁾ *t*-tests, ⁽²⁾ one-way ANOVA, ⁽³⁾ number of observations = 43, 25, 18, 5, 4, 11, 23, respectively.

$P < 0.001$), and other descriptors related to the presence of young foliage. However, the strongest correlation occurred between the scores and the total number of arthropods within the samples ($r = 0.450$, $P < 0.001$). A close inspection of the original data matrix revealed that high-scoring samples were strongly dominated by certain species, whereas lower-scoring samples were more uniform in their taxonomic composition. Hence, this axis was interpreted as a measure of the aggregation ability of arthropods, and its influence on their spatial distribution. Corylophidae, Aphelinidae, Formicidae and Psylloidea, for example, were restricted to, and aggregated in, only a few samples. In contrast, Araneae and certain Psocoptera were more evenly distributed. The first two components of the ordination are positively correlated ($r = 0.569$, $P < 0.001$) and this suggests that as the proportion of young foliage in the samples increases, taxa tend to aggregate within these samples. Immature stages usually scored more on this axis than did the corresponding adults, probably reflecting the aggregation of egg batches.

The third axis explained 11.2% of the variance and could not be adequately explained by the foliage attributes recorded (inset of Fig. 1b), although a positive correlation existed with air temperature ($r = 0.277$, $P < 0.001$). A plot of the samples, with the time at which they were performed as indices, segregated morning and afternoon samples. Therefore this axis was interpreted as the effect of arthropod activity on the sampling. Samples obtained later in the day, at higher temperatures, included more Psocoptera and Nematocera.

The fourth axis explained 9.4% of the variance and a weak correlation existed only between the sample ordination scores and the variable AXIS ($r = 0.171$, $P < 0.05$). The plot of the taxa suggests an increasing relation with the subcortical habitat: high-scoring Gryllidae, Curculionidae, Blattodea, etc., are associated with the trunks of trees rather than the foliage and were often observed foraging on this substrate. Spider families were segregated along this axis into subcorticolous taxa (Thomisidae, Clubionidae) and foliage taxa (Salticidae, Theridiidae,

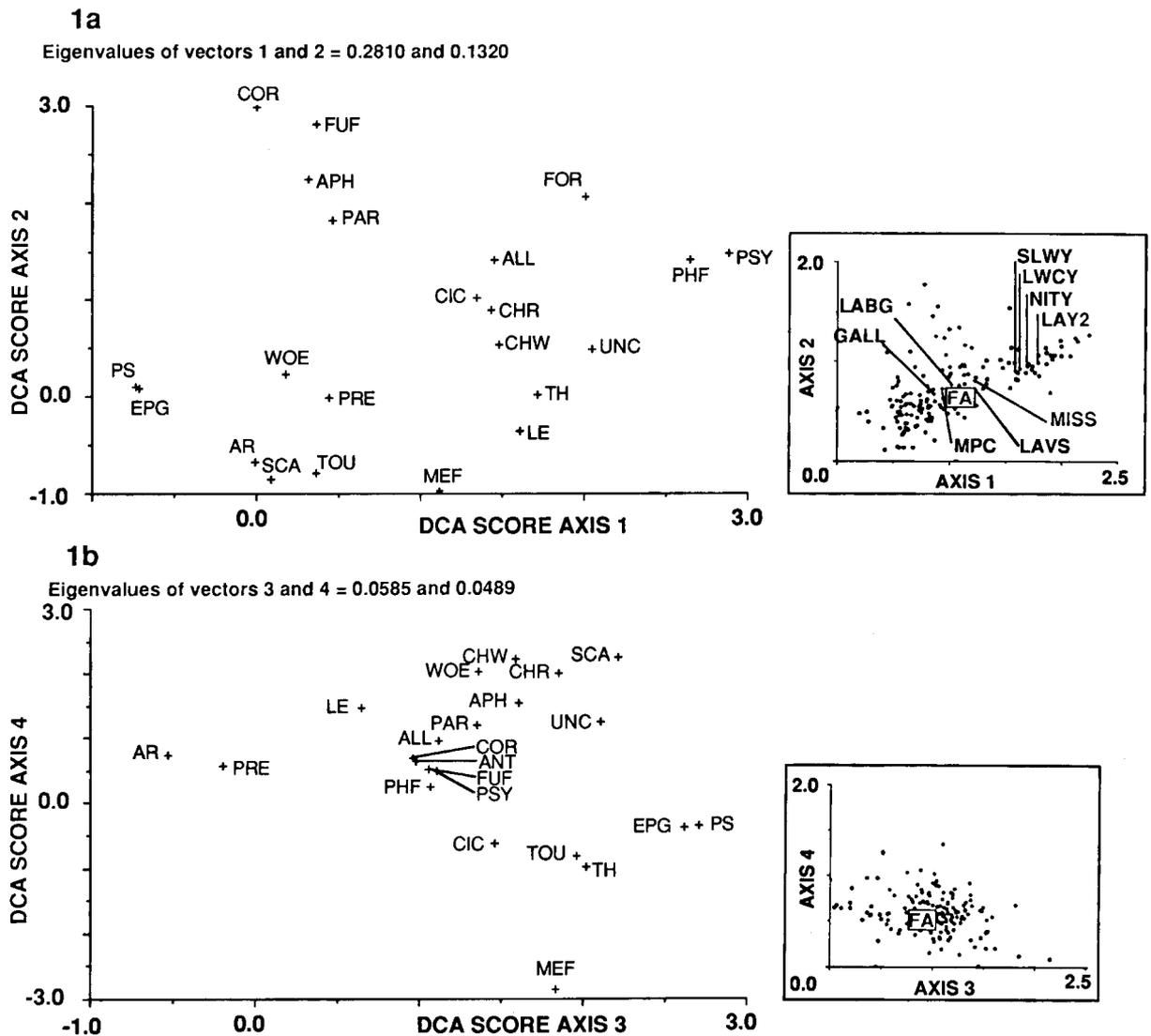


Fig. 1. Hybrid ordination of the abundance of forty-five arthropod taxa obtained by 160 fogging samples. Plots in the spaces formed by axes 1, 2 (1a) and axes 3, 4 (1b). The extended plots refer to the first ordination (samples-by-taxa matrix; coding variables as in Table 4), whereas the smaller plots (in inset) refer to the second ordination (samples-by-foliage attributes matrix; 'FA' refers to the position of remaining attributes, not plotted).

Araneidae). However, there is little direct evidence for the interpretation of the fourth axis, since the distance to the trunk was not recorded when performing the fogging. The high score of chrysomelid beetles on this axis nevertheless suggests that some taxa may seek protection from enemies or climatic conditions by taking shelter in bark microsites (the thick, scaly and cracked bark of *A. actinophyllum* trunks is adequate for that purpose and often remains dry in the crown during rainy periods). The fourth component of the ordination was negatively correlated with the third component ($r = -0.275$, $P < 0.001$) and the following interpretation of this relation is offered: as the activity of certain arthropods increases (favourable periods for feeding bouts, optimum air temperature and humidity,

etc.), they move away from the subcortical habitat and become more exposed to fogging. When activity decreases, these taxa move again closer to the trunk interface.

In general, the new combination of foliage attributes in multiple regression analyses explained only a small fraction of the variance in the abundance of most arthropod groups (usually less than 30%, with the regression not even being significant for some groups: Table 3). However, a higher proportion of the variance was explained for phloem-feeders, and particularly for psyllids, for which the index of food quality accounted for more than 50% of the variance. Foliage age and climatic conditions were important factors for a number of groups, while the activity index slightly influenced the distribution of subcortical taxa.

Table 3. Stepwise multiple regression analyses on the abundance of arthropods, grouped into arboreal guilds, in 160 fogging samples. For each entry the upper value refers to the parameter estimate, the lower to partial R^2 , except for the regression where they refer to F -test and R^2 respectively.

Guild	Intercept	FQI ⁽¹⁾	CLIM ⁽²⁾	ACTI ⁽³⁾	OLDF ⁽⁴⁾	Regression
All arthropods	0.9832	1.7614	1.1531	n.s.	0.5611	21.08
		0.1579	0.0760	—	0.0546	0.2883
Chewers	-0.0431	1.6035	0.5158	0.7832 [†]	0.5843 [†]	10.05
		0.1233	0.0560	0.0152	0.0115	0.2059
Epiphyte grazers	-0.1147	-1.3822	0.5051	1.0971	1.4251	9.40
		0.0586	0.0374	0.0191 [†]	0.0800	0.1952
Fungal-feeders	0.0122	n.s.	n.s.	n.s.	1.3675	10.00
		—	—	—	0.0595	0.0595
Phloem-feeders	0.1052	4.8869	0.3775 [†]	n.s.	1.2904	53.08
		0.4669	0.0095	—	0.0287	0.5051
Parasitoids	0.2809	n.s.	0.5275	-0.9839	0.7777	6.45
		—	0.0585	0.0242	0.0276	0.1104
Predators	0.6286	n.s.	0.3791	0.9167	n.s.	5.93
		—	0.0433	0.0269	—	0.0703
Uncertains	-0.0050	2.2452	n.s.	n.s.	1.2329	25.81
		0.2002	—	—	0.0472	0.2474
Ants	0.0523	0.4204	0.3102	n.s.	n.s.	4.01
		0.0174	0.0311	—	—	0.0486

Regression not significant for mesophyll-feeders, scavengers, wood-eaters and tourists. All parameter estimates significant with alpha-to-enter = 0.05, [†] significant with $\alpha = 0.15$.

$$^{(1)} \text{ FQI} = \alpha 1 \times (\text{LAY1})^{\beta 1} + \alpha 2 \times (\text{LAY2})^{\beta 2} + \alpha 3 \times (\text{LWCY})^{\beta 3} + \alpha 4 \times (\text{NITY})^{\beta 4}.$$

$$^{(2)} \text{ CLIM} = \text{TMAX} \times ((\text{TMAX} - \text{TMIN}) \times (\text{RAIN} + 0.5))^{-1}.$$

$$^{(3)} \text{ ACTI} = \alpha 5 \times (\text{TEMP})^{\beta 5} + \alpha 6 \times (\text{BRAR} \times \text{LAT}^{-1})^{\beta 6} + \alpha 7 \times (\text{AXIS})^{\beta 7}.$$

$$^{(4)} \text{ OLDF} = \alpha 8 \times (\text{HEIG})^{-\beta 8} + \alpha 9 \times (\text{MINE})^{\beta 9} + \alpha 10 \times (\text{MPC})^{\beta 10}.$$

Arthropod abundance and distribution

In total, over 5500 arboreal arthropods were collected by restricted canopy fogging from Black Booyong foliage. Table 4 details arthropod abundance within trees (lower and upper crown), between trees, and between samples of young and mature foliage. These data, along with computing of coefficients of variation and two-way ANOVAs, suggest that between-tree variance in arthropod abundance was generally more marked than within-tree variance. Compass orientation had a negligible effect on arthropod distribution and few arthropods exhibited marked preferences for a certain stratum within the crown. Fungal-feeders, and particularly corylophids, were more abundant in the lower canopy, where the epiphyll load of leaves was higher and where the branches remained wet for longer during rainy periods. In contrast, epiphyte grazers (mostly psocids) were not so markedly distributed in the lower sections of the crown and juvenile psocids were even slightly more numerous in the upper level. Thermophilous chrysomelid beetles were more abundant in the upper canopy. Chewers (particularly caterpillars) and tourists were slightly more abundant in the upper canopy and these observations were close to statistical significance. Corylophidae, Clubionidae, Theridiidae, Cicadellidae and

Lepidoptera exhibited low variance between study trees. Variance in arthropod numbers was generally similar in the lower and in the upper canopy. In general, arthropod abundance on Black Booyong was higher on young foliage than on mature foliage and most herbivores were restricted to young foliage, conforming to their observed feeding patterns and seasonality (Basset, 1989, 1991a). However, cicadellids and chrysomelids were not so conspicuously associated with young leaves (in the latter case, *Longitarsus* sp., which was extremely common in mature foliage samples, appears to feed rarely either on mature or young leaves and its feeding habit remains unknown). In contrast, epiphyte grazers, parasitoids and spiders were more abundant on mature foliage. Ants were dependent on the presence of young leaves and the concomitant increase of potential prey and psyllid honeydew, but their abundance on *A. actinophyllum* foliage was low (Basset, 1991b).

Discussion

Habitat heterogeneity of rainforest trees

Although the number of trees examined in detail was low, trends emerging from the within-tree analysis of

Table 4. Distribution of selected guilds and taxa (coding variable) per stratum, tree and per young and mature foliage samples. Mean (SE) number of individuals collected per fogging sample.

Guild/taxa	Lower (n = 122)	Upper (n = 118)	(1)	Tree 7 (n = 32)	Tree 8 (n = 32)	Tree 9 (n = 32)	Tree 10 (n = 32)	(2)	Young (n = 49)	Mature (n = 79)	(3)
All arthropods (ALL)	23.75 (1.50)	22.82 (1.32)	n.s.	28.40 (2.41)	21.50 (2.05)	34.56 (3.90)	30.18 (3.65)	*	36.57 (3.27)	23.75 (1.33)	***
Chewers (CHW)	1.46 (0.19)	2.02 (0.24)	n.s.	1.78 (0.55)	1.78 (0.35)	3.56 (0.57)	2.40 (0.41)	**	3.14 (0.50)	1.91 (0.24)	*
Epiphyte grazers (EPG)	1.91 (0.25)	2.24 (0.32)	n.s.	4.37 (0.85)	3.18 (0.61)	3.12 (0.49)	1.18 (0.27)	**	1.36 (0.24)	3.96 (0.45)	***
Fungal-feeders (FUF)	2.06 (0.36)	0.87 (0.15)	**	3.09 (0.48)	1.47 (0.38)	1.31 (0.47)	1.84 (0.52)	n.s.	1.94 (0.45)	1.92 (0.48)	n.s.
Phloem-feeders (PHF)	5.50 (1.02)	4.92 (0.68)	n.s.	3.53 (0.60)	2.28 (0.36)	3.03 (3.28)	11.50 (2.25)	***	15.51 (2.40)	2.67 (0.29)	***
Parasitoids (PAR)	1.31 (0.13)	1.14 (0.13)	n.s.	2.34 (0.35)	1.59 (0.26)	1.44 (0.24)	0.75 (0.17)	***	0.96 (0.16)	1.89 (0.19)	***
Predators (PRE)	7.57 (0.38)	7.39 (0.50)	n.s.	9.13 (1.41)	7.18 (0.86)	8.34 (0.71)	6.56 (0.68)	n.s.	7.61 (0.65)	7.92 (0.67)	n.s.
Scavengers (SCA)	0.66 (0.09)	0.56 (0.09)	n.s.	0.81 (0.14)	0.44 (0.13)	0.44 (0.24)	0.44 (0.11)	*	0.51 (0.16)	0.54 (0.08)	n.s.
Tourists (TOU)	0.29 (0.05)	0.48 (0.08)	n.s.	0.28 (0.08)	0.28 (0.12)	0.12 (0.07)	0.31 (0.10)	n.s.	0.25 (0.07)	0.25 (0.06)	n.s.
Uncertains (UNC)	1.66 (0.21)	1.86 (0.26)	n.s.	1.25 (0.30)	2.03 (0.40)	1.59 (0.46)	3.75 (0.79)	**	3.69 (0.58)	1.20 (0.19)	***
Wood-eaters (WOE)	0.34 (0.05)	0.45 (0.07)	n.s.	0.66 (0.18)	0.19 (0.08)	0.34 (0.09)	0.53 (0.13)	n.s.	0.28 (0.07)	0.51 (0.10)	n.s.
Mesophyll-feeders (MEF)	0.84 (0.12)	0.83 (0.09)	n.s.	0.88 (0.21)	1.00 (0.29)	1.15 (0.23)	0.81 (0.21)	n.s.	1.22 (0.24)	0.80 (0.11)	n.s.
Ants (ANT)	0.61 (0.12)	0.42 (0.09)	n.s.	0.47 (0.19)	0.28 (0.09)	1.47 (0.39)	0.31 (0.15)	**	1.10 (0.28)	0.34 (0.07)	*
Araneae (AR)	5.63 (0.32)	6.11 (0.48)	n.s.	7.49 (1.43)	5.50 (0.72)	5.84 (0.57)	4.18 (0.49)	n.s.	4.40 (0.41)	6.58 (0.67)	**
Chrysomelidae (CHR)	0.99 (0.12)	1.63 (0.22)	*	1.18 (0.25)	1.56 (0.36)	2.94 (0.48)	1.72 (0.39)	**	2.18 (0.34)	1.64 (0.23)	n.s.
Corylophidae (COR)	1.77 (0.36)	0.54 (0.14)	**	3.00 (0.49)	1.31 (0.36)	1.03 (0.48)	1.28 (0.46)	n.s.	1.49 (0.43)	1.76 (0.48)	n.s.
Cicadellidae (CIC)	1.06 (0.13)	1.05 (0.12)	n.s.	1.12 (0.19)	1.09 (0.31)	1.69 (0.29)	0.97 (0.20)	n.s.	1.47 (0.24)	1.06 (0.15)	n.s.
Psylloidea (PSY)	4.44 (0.98)	3.68 (0.65)	n.s.	2.19 (0.52)	1.38 (0.30)	11.38 (3.19)	10.19 (2.24)	**	13.94 (2.35)	1.53 (0.25)	***
Aphelinidae (APH)	0.42 (0.09)	0.29 (0.06)	n.s.	1.03 (0.29)	0.62 (0.14)	0.44 (0.13)	0.22 (0.07)	*	0.20 (0.06)	0.81 (0.14)	***
Lepidoptera (LE)	0.32 (0.05)	0.50 (0.08)	n.s.	0.28 (0.08)	0.22 (0.09)	0.53 (0.18)	0.53 (0.13)	n.s.	0.61 (0.14)	0.25 (0.05)	**
Psocoptera (PS)	1.39 (0.22)	1.64 (0.28)	n.s.	3.81 (0.79)	2.31 (0.52)	2.47 (0.39)	0.91 (0.22)	**	1.04 (0.19)	3.20 (0.40)	***
Thysanoptera (TH)	2.35 (0.26)	2.11 (0.22)	n.s.	1.72 (0.30)	0.66 (0.52)	2.28 (0.55)	3.88 (0.55)	***	4.08 (0.54)	1.70 (0.16)	***

(1) Followed by *t*-tests on all sampling events. (2) Followed by one-way ANOVA on sampling events 2 and 3. (3) Followed by *t*-tests on sampling events 2 and 3.

foliage attributes are clear and are linked with arthropod spatial distribution within these trees. A constraint of this study was the physical restriction of access and sampling to the inner core of tree crowns. This increased pseudo-replication and, by necessity, the present discussion comments upon part of the crown only. Variances of foliage attributes within and between study trees were high and emphasized the heterogeneity of the rainforest tree studied. This would have probably been even more marked if access and regular sampling in the uppermost leaf layer of trees would have been possible. Although the size of the leaves and their epiphyll load appeared to account for much of the heterogeneity of the mature foliage to human eyes, internal foliar characteristics, their relation with the magnitude of leaf production and their seasonal changes may be more important for rainforest herbivores.

When all arthropods were considered together, about 55% and 30% of the variance in abundance was explained by the leaf traits recorded, in detrended correspondence analysis and multiple regression analysis, respectively. Hodkinson & Casson (1987), visually recording the abundance and feeding punctures of Hemiptera in the understorey of a rain forest in Sulawesi, observed very few correlations between their censuses and selected leaf characteristics. It is probable that microclimate effects play an important role in the spatial distribution of rainforest arthropods (e.g. Sutton, 1989), but investigation of them was beyond the scope of this work. They may be responsible for the aggregational aspects of arthropod distribution on rainforest vegetation and may prevail over other parameters such as leaf size and foliage compactness, particularly on mature foliage.

Arthropod spatial distribution

Arthropod spatial distribution on Black Booyong revealed three distinct patterns. Firstly, the distribution of most herbivorous taxa (though not some mesophyll-feeders) was related to the abundance of young leaves and their food quality (i.e. their nitrogen and water content) and was negligibly affected by leaf size and foliage compactness (setting aside chemical defences other than fibre). Foliar nitrogen is particularly low in Black Booyong and probably acts as a limiting factor for associated herbivores such as phloem-feeders. On this tree, herbivore foraging for optimal food abundance and quality may prevail over foraging for dense foliage in order to escape predators. This is likely, because the foliage of this tree consists of densely packed compound-leaves and, furthermore, predation pressure from arboreal ants appears to be low (as evaluated by the abundance of these insects on the foliage).

Secondly, the distribution of some taxa was dependent on the presence of older and shaded foliage, with high epiphyll load (epiphyte grazers, psocid nymphs, fungal-feeders and corylophids). Southwood *et al.* (1982) noted that the structural feature of trees in Britain and South Africa which correlated best with the abundance of arboreal communities, was the epiphyll load and its influence on epiphyte grazer populations. Thirdly, the distribution

of remaining guilds and taxa was not consistently explained by any of the foliage attributes recorded, except for air temperature, which influenced arthropod activity. In these cases, arthropod behaviour not directly related with leaf traits probably influence arthropod distribution. Turchin (1987), for example, showed that the movement of Mexican bean beetles is aggregative: beetles are more likely to move towards plants occupied by conspecifics. Barnard *et al.* (1986) reported that the distribution of some Neuroptera and Raphidioptera on oak foliage in England was affected by the distance to the trunk, some species preferring to remain near this area. They attributed this observation to camouflage behaviour.

The first two patterns emphasize that light, which is a limiting factor for leaf production, indirectly affects the spatial distribution of several arthropod groups, whereas the third pattern may emphasize the roles of microclimate and of interaction with conspecifics on the distribution of rainforest arthropods.

Arthropod stratification was not marked within the inner volume of Black Booyong crowns. Although vertical stratification has been reported for a number of insect species, it is well documented that herbivores are rarely completely absent from any crown section and level (Lawton, 1983). In the rainforest canopy, arthropod distribution patterns may be dependent on many environmental parameters, not directly related to the height above the ground, such as tree illumination (resulting from local gaps, crown orientation, topography, etc.), aerial currents and surrounding vegetation (conspecific host-trees or suitable habitats nearby). Consequently, in rainforest environments, these factors may prevail over, or overshadow, host-resistance induced by host maturation processes, which, for example, have been found important for certain temperate herbivores (Kearsley & Whitham, 1989). Arthropod stratification within the inner crown of rainforest hosts may be conspicuous only when certain light conditions are met, namely when illumination differs greatly between the lower and upper crown. On *A. actinophyllum*, subjective impression, as well as limited sampling in crown sections other than the inner core, suggests that arthropod abundance and activity in the outer periphery of the crown may not be extremely different from that in the inner core. However, an abrupt transition in arthropod abundance, particularly in that of insect herbivores, may occur between the uppermost leaf layer and subjacent leaf layers of emergent trees. This may result from both the overabundance of young leaves and the curved aspect of mature leaves in the uppermost leaf layer. This bending, which is caused by low turgor potentials (e.g. Doley *et al.*, 1988), may protect arthropods from weather, desiccation and predators. Future work on the arthropod fauna of the rainforest canopy should aim at investigating the fascinating habitat represented by this ecotone.

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