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Influence of leaf traits on the spatial distribution of insect herbivores associated with an overstorey rainforest tree

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Summary. The spatial distribution of insect herbivores associated with the Australian rainforest tree *Argyrodendron actinophyllum* (Sterculiaceae) was investigated by restricted canopy fogging. The foliage of this species was low in nitrogen and water content, and high in fibre content. Herbivore abundance was positively correlated with the amount of young foliage present within the samples and in adjacent samples, and with the nitrogen content of young leaves. In particular, the occurrence of phloem-feeders was correlated with the magnitude of translocation within the samples. The influence of leaf water content upon herbivore distribution was marginal, presumably because this factor is not limiting in rainforest environments during the wet season, which usually coincides with the season of leaf-flush. Specific leaf weight, leaf size and foliage compactness had little or no apparent effect on herbivore distribution. Since the magnitude of leaf turnover affected both the quantity and the quality, as exemplified by translocation effects, of young foliage available, this factor may be critical to herbivores associated with evergreen rainforest trees which are particularly low in foliar nutrients, such as *A. actinophyllum*.

Key words: Insect-plant interactions – Leaf water content – Nitrogen – Rain forest – Translocation

The field distribution of insect herbivores in temperate woodlands has been documented and related to several features of their host-plants. In particular, leaf nutrients and defence characteristics play a major role in determining herbivore food choice, abundance and distribution (review in Strong et al. 1984). For example, a positive relationship between foliar nitrogen and herbivore abundance has been demonstrated for numerous taxa, particularly for phloem-feeders (review in Mattson 1980). Foliar nitrogen primarily affects the growth rate of herbivores (e.g. Wint 1983) and their fecundity (e.g. Ohmart et al. 1985). Other important factors influencing the field distribution of temperate herbivores include digestibility-reducers such as tannins, phenols and fibre (e.g. Feeny 1970; Fox and Macauley 1977; Mattson and Scriber 1987); toxins such as alkaloids (e.g. Strong et al. 1984); water content (e.g. Feeny 1976; Scriber 1977); leaf toughness and structure (e.g. Feeny 1970; Mooney and Gulmon 1982).

Determinants of the spatial distribution of tropical herbivores are not so well known. Most workers have studied this subject within the shrub layer of rain forests and were able to relate herbivore preferences to leaf age and to interspecific differences in chemical defences and in successional status of their food-plants (Coley 1983; Janzen and Waterman 1984; Hodkinson and Casson 1987; Aide 1988). Intraspecific studies of food-plants and their associated herbivores further emphasized the importance of leaf expansion rates (Aide and Londoño 1989), habitat (Ernest 1989), host illumination regime (Harrison 1987) and the concomitant changes in plant defences (e.g. Macedo and Langeheim 1989). To date, most studies of arboreal insect herbivores in rain forests have focused on temporal distribution and differences between forest types (e.g. Wolda 1978; Erwin 1983). There is an almost complete lack of information about the intraspecific distribution of herbivores associated with overstorey rainforest trees and it is not known to which extent these herbivores follow the trends described for their counterparts foraging within the shrub layer.

The arthropod fauna of the overstorey rainforest-tree *Argyrodendron actinophyllum* in Australia has been the subject of detailed investigations (Basset 1989, 1990, 1991a, b). In particular, it was shown that considerable variance in arthropod spatial distribution could be attributed to leaf age characteristics, arthropod aggregation patterns, arthropod activity and distance to tree trunk. Furthermore, herbivore distribution was mainly restricted to patches of young foliage (Basset in press). The present contribution explores more specifically the

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spatial distribution of herbivores associated with *A. actinophyllum* in relation to young-foliage characteristics. The purpose of the study was to test the prediction that spatial heterogeneity within rainforest tree-crowns is high and contributes much to herbivore aggregation on highly nutritive foliage sites. This prediction was tested by relating the abundance of herbivores to selected leaf traits thought to be representative of leaf quality and of leaf structure. Specifically, the following questions were asked: (a) is the nutritive value of the foliage of *A. actinophyllum* high for insect herbivores; and (b) what is the most consistent predictor of herbivore abundance among measured leaf traits?

Methods

Study site and host-tree

The study was conducted in a stand of complex notophyll vine forest (warm subtropical rain forest), at Mount Glorious, near Brisbane, Australia (27° 19′ 20″ S, 152° 44′ 55″ E, altitude 700 m). Young (1985) provides an account of the floristics of the site, which is described further in Basset (1989). *Argyrodendron actinophyllum* (Bailey) Edlin ("Black Booyong", Sterculiaceae) grows to 50 m high and is a dominant canopy species. Its main features include plank buttresses, scaly bark and palmate leaves with domatia. Black booyong is an intermittently growing evergreen tree and leaf production is synchronous between individuals during the wet summer (October to February; Basset 1989).

Herbivore sampling

Insect herbivores were collected by "restricted canopy fogging" (Basset 1990). Briefly, this sampling method involved fogging with CO_2 0.7 m^2 of foliage enclosed by a plastic frame. Canopy access was provided by single rope techniques and was restricted to the inner core of tree crowns, where sampling was performed (the outer periphery of the crown was not sampled and the highest samples obtained were from 3–4 m below the top leaf layer). All fogging was performed during day-time on dry foliage and samples did not include flowering and fruiting plant material, which was generally scarce during the study. Firstly, 80 samples were collected in ten different mature trees during January–February 1987 (Trees 1–10). This pilot study allowed the design of a sampling programme for four trees (Trees 7–10), which took place during three other sampling events in April–May 1987, November–December 1987 and January–February 1988 (160 samples). For a given sampling event, 16 samples were performed within each tree. They consisted of 8 samples from the lower crown (15–25 m) and 8 samples from the upper crown (25–35 m), which were taken from each of the four possible access points within the crown (four lines orientated N-S-E-W). Anaesthetized insects were collected in 70% ethanol, sorted to morphospecies, examined by various taxonomists and deposited at the Queensland Museum, Brisbane. The taxonomic composition of the arthropod fauna foraging within the crowns of *A. actinophyllum* is described in Basset (1990, 1991a).

Leaf characteristics

The leaf turnover of study trees during the sampling events was estimated visually (variable TURN; % young leaves present) and the air temperature (TEMP) was recorded during fogging. From leaf samples, several biophysical attributes of foliage, which are fully listed elsewhere (Basset in press), were recorded separately for young and mature leaves. Leaves were counted (i.e., variable NLEVY: number of young leaves within the sample) and measured in order to estimate from mathematical regressions total sample size, area of young leaves within the sample and area of young leaves within four adjacent samples (variables LAT, LAY and ADJF; Basset 1989). Other leaf attributes included visual estimations of apparent leaf damage, epiphyll load and measurements of foliage compactness (point quadrat method: Warren Wilson 1963). Leaf sub-samples were harvested to determine leaf water content and leaf weight per unit fresh weight (variables LWCY and SLWY; determined by oven-drying), total foliar nitrogen per unit dry weight (variable NITY, determined by the Kjeldahl technique with a colorimetric method: Williams and Twine 1967) and total percentage fibre per unit dry weight (variable ADFM; acid detergent fibre method: Van Soest 1963). The intensity of the translocation (Pate 1980; variable TRANS) within samples was expressed as young-leaf nitrogen minus the corresponding value for mature leaves (scaled to positive value). Particular emphasis is given in the present paper to 49 samples obtained from Trees 7–10, which consisted partly of young foliage.

Statistical methods

Since sample size had some influence on the number of arthropods collected within the subset of samples including young foliage, arthropod abundances were corrected and expressed per unit sample size. Most nutritive and structural features of foliage were strongly inter-related (Basset 1989) and this situation complicates the analysis of their respective influences on herbivore distribution. For this reason, multiple regression analysis was not attempted. Instead, the strength of relationships between leaf traits and herbivore abundance was firstly estimated by the Pearson correlation-coefficient [data $\ln(x+1)$ transformed]. Secondly, the causal relationships of these correlations were investigated with path analysis, which allows the separation of direct and indirect components of a correlation coefficient (Sokal and Rohlf 1981; data $\ln(x+1)$ transformed and standardized). Means are expressed with their standard errors throughout the text.

Results

Black booyong leaves as a food resource for folivores

Average values of black booyong foliar nitrogen and leaf water were low, while fibre content was high (Table 1). Young leaves were higher in water and nitrogen content than mature leaves ($t = 18.55$, $P < 0.001$ and $t = 2.43$, $P < 0.05$, respectively) and lower in specific leaf weight ($t = 13.15$, $P < 0.001$). The percentage fibre in young leaves appeared to be similar to that in mature leaves, but this is not certain because few young leaves were analysed ($t = 0.66$, n.s., $n = 6$). The negative correlations between the specific leaf weight of young leaves and their water and nitrogen content ($r = -0.873$ and -0.772 respectively, $P < 0.001$) account for the lower food quality in maturing leaves. Similarly, positive correlations emphasize leaf maturation processes, such as the relationship between specific leaf weight and nitrogen of mature leaves ($r = 0.508$, $P < 0.001$) and the relationships between leaf nitrogen and water content ($r = 0.739$ and 0.729 for young and mature leaves respectively, $P < 0.001$). Although few samples of young leaves were obtained during late summer, a strong decline in nitrogen content of young leaves was apparent during this period

Table 1. Foliar characteristics of black booyong. Means of attributes (1 SE) recorded of 160 samples obtained from four trees

Attribute	Mean	Range	Strata (a)	Trees (b)
Total leaf area of sample (cm^2) (c)	3486 (82.3)	1760 – 6063	n.s.	***
Total leaf area of young foliage (cm^2)	294.1 (64.6)	0 – 4646	n.s.	***
Mean length of largest leaflet (cm)	9.10 (0.14)	5.5 – 13.9	***	***
Epiphyll load (%)	11.33 (0.59)	1.4 – 46.0	***	***
Apparent leaf damage (%)	11.22 (0.43)	2.4 – 30.3	n.s.	***
Water content – Y (% FW)	65.3 (0.64)	58.5 – 70.9	n.s.	n.s.
Water content – M (% FW)	52.9 (0.23)	46.5 – 61.9	n.s.	***
Specific leaf weight – Y (10^{-4} g cm^{-2})	67.5 (2.34)	44.1 – 95.5	n.s.	**
Specific leaf weight – M (10^{-4} g cm^{-2})	100.9 (1.07)	74.6 – 139.8	***	***
Total nitrogen – Y (% DW)	1.80 (0.07)	1.03 – 2.70	*	n.s.
Total nitrogen – M (% DW)	1.62 (0.02)	0.03 – 2.12	n.s.	***
Total fibre – Y (% DW)	53.42 (2.10)	45.2 – 59.1	–	–
Total fibre – M (% DW)	54.70 (0.37)	47.7 – 62.7	n.s.	n.s.

* $P \leq 0.05$ ** $P \leq 0.01$ *** $P \leq 0.001$ n.s. not significant
Y = young leaves, M = mature leaves

[a] *t*-tests between crown strata: 15–25 m and 25–35 m
[b] One-way ANOVA between trees
[c] Leaves considered one-sided

Table 2. Correlation coefficients between the abundance of selected herbivore groups and foliage attributes of samples including young leaves

Guild/Taxa	TEMP	ADJF	LAT	TURN	LAY	NLEVY	LWCY	SLWY	NITY	ADFM	TRANS
Chewers	–	n.s.	–	–	–	–	n.s.	n.s.	0.315	–	–
Chewers (a)	–	0.361	–	0.287	0.303	0.370	0.338	0.319	0.386	n.s.	0.344
Phloem-feeders	–	0.612	–	0.663	n.s.	0.602	n.s.	–	0.380	–0.355	0.389
All herbivores	–	0.541	–	0.482	n.s.	0.514	0.289	–	0.397	–0.368	0.365
Chrysomelidae	0.286	–	–	–	–	–	–	–	–	–	–
Curculionidae (b)	–	n.s.	–0.504	–	–	–	–	–	–	–	–
Psylloidea	–	0.596	–	0.684	–	0.598	0.297	–	0.409	–0.393	0.408
Psylloidea (c)	–	0.636	0.348	0.542	0.425	0.471	0.478	0.461	0.555	–0.283	0.550
Cicadellidae	–	–	0.313	–	–	–	–	–	–	–	n.s.
Cicadellidae (c)	–	–	0.363	–	–	–	–	–	–	–	–
Thysanoptera (c)	–0.293	–	–	–	0.304	n.s.	n.s.	n.s.	0.313	–0.349	0.312
Lepidoptera (b)	–	n.s.	–	–	–	–	–	–	n.s.	–	–

TEMP = temperature; ADJF = adjacent young foliage; LAT = total leaf area; TURN = leaf turnover; LAY = area of young foliage; NLEVY = No. young leaves; LWCY = leaf water; SLWY = specific leaf weight; NITY = total nitrogen; ADFM = fibre; TRANS = translocation

(a) biomass; (b) chewers only; (c) nymphs only.
All coefficients significant to at least $P < 0.05$, n.s. = approaching significance

(early summer: 1.89 ± 0.07% DW, $n = 30$; late summer: 1.26 ± 0.09, $n = 4$; $t = 3.21$, $P < 0.01$). Leaf traits were generally more variable among study trees than between the lower and upper crowns of trees (Table 1). In particular, nitrogen of mature foliage was significantly different between study trees. Foliar tannins and phenols could not be investigated in this study and black booyong foliage appears to lack alkaloids (Webb 1952).

Predictors of herbivore abundance

In total, over 5500 arthropods were collected by restricted canopy fogging. Most phloem-feeders associated with black booyong were host-specific psyllids, whereas most chewers were generalists (Basset 1989). Most herbivores were spatially restricted to young foliage, as were their feeding activities and their seasonal occurrence (Basset 1991b, in press). Table 2 shows, for young foliage samples, the Pearson correlation coefficients between selected herbivore taxa and foliage attributes. The best predictor of herbivore abundance in the samples was the amount of young foliage available (leaf turnover, area and number of young leaves; variables TURN, LAY and NLEVY in Table 2), and particularly the amount of young foliage present in adjacent samples (ADJF). By contrast, none of the variables related to foliage compactness (sample compactness, leaf size, area of small leaves, etc.) had any influence on herbivore abundance. The abundance of chrysomelid beetles was not related to the dietary quality of leaves, but to a factor dependent on sample size, namely the number of leaves (young and mature) present within the sample ($r = 0.448$, $P < 0.001$), and to a lesser extent, to air temperature (TEMP, Table 2). The second-best predictor of herbivore abundance was the nitrogen content of young leaves. In particular, translocation effects, as defined in this study, were affected by the magnitude of leaf turnover in the study trees (Table 3, $r = 0.990$, $P < 0.05$) and had significant effects on phloem-feeder abundance (Table 2). Fibre content of mature leaves was negatively correlated with herbivore abundance on adjacent young leaves. Leaf water content appeared to be less critical than nitrogen for herbivores, as was specific leaf weight (Table 2).

Table 3. Herbivore loads (mean numbers of individuals collected per sample, with 1 SE in brackets) and environmental parameters measured on four trees extensively sampled

Variable	Tree 7	Tree 8	Tree 9	Tree 10	ANOVA
Chewer load	1.78	1.78	3.56	2.40	4.42**
	(0.55)	(0.35)	(0.57)	(0.41)	
Phloem-feeder load	3.53	2.28	13.03	11.50	10.04***
	(0.60)	(0.36)	(3.28)	(2.25)	
Herbivore load (total)	6.28	5.59	18.30	15.74	8.32***
	(0.75)	(0.67)	(3.29)	(2.44)	
Nitrogen (young leaves, % DW)	1.63	1.37	1.67	1.95	1.64 n.s.
	(0.01)	(0.10)	(0.06)	(0.12)	
Translocation (% DW)	0.68	0.64	1.53	2.10	6.13*
	(0.37)	(0.32)	(0.19)	(0.23)	
Leaf turnover (%)	7.5	2.5	20.0	30.0	–
Crown openness (%) ([a])	55	80	50	70	–

* $P \leq 0.05$ ** $P \leq 0.01$ *** $P \leq 0.001$ n.s. not significant

([a]) Proportion of ground area covered by vertical projection of foliage: low values relate to high crown illumination

Since herbivore distribution was invariably linked with the presence and the local abundance of young foliage within trees, herbivore abundance often differed markedly from one cluster of branches to another. Restricting the data set to young foliage samples showed that herbivore loads differed between study trees (Table 3). On a larger scale, herbivore abundance was not significantly different between the lower and upper crowns of trees (Basset in press). Chrysomelids did not follow this trend and their abundance was significantly higher in the upper crown than in the lower crown (mean no. individuals collected per sample 0.99 ± 0.12 and 1.63 ± 0.22, respectively, $t=2.54$, $P<0.05$). Furthermore, a significant difference in chrysomelid loads was detected between the most illuminated (Tree 9: 2.94 ± 0.48) and the most shaded (Tree 8: 1.18 ± 0.25) of the study trees ($t=2.30$, $P<0.05$).

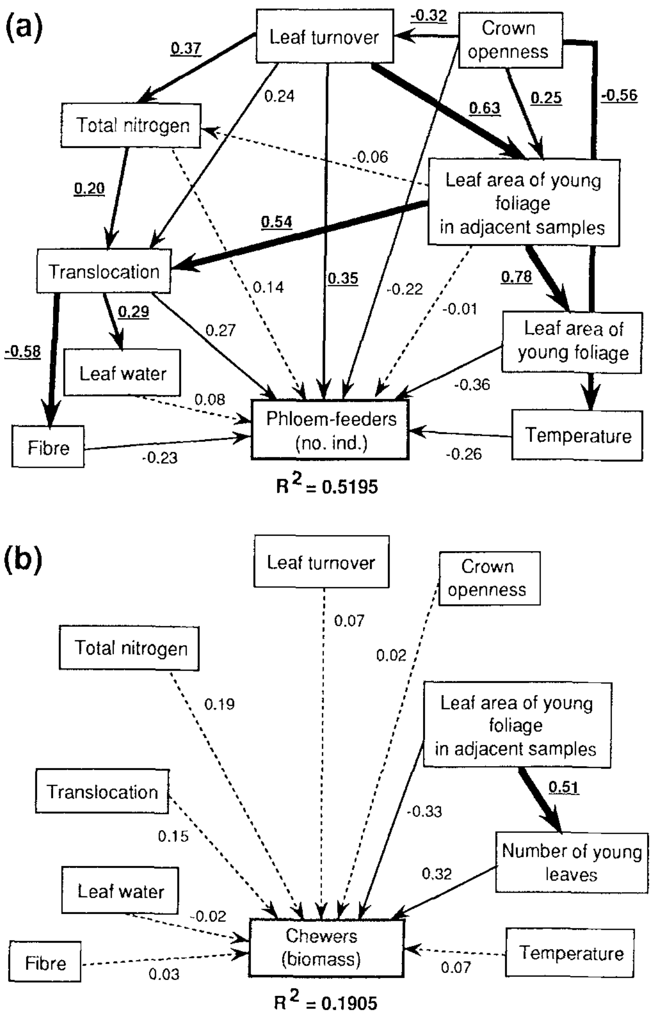

Fig. 1a, b. Results of path analysis with particular emphasis on dependent variables **a** the number of phloem-feeders and **b** the biomass of chewers. Significant path coefficients ($P<0.05$) are *underlined*

Path analysis revealed more explicitly (Fig. 1) that 52% of the variance in the abundance of phloem-feeders could be accounted for by leaf turnover, and to a lesser extent, by leaf area of young foliage, translocation, air temperature, fibre content and crown openness. Only 19% of the variance in the biomass of chewers could be accounted for, mostly by non-significant paths originating from the area and the number of young leaves. The analysis further indicated significant paths from, among others, leaf turnover to the amount of young foliage in adjacent samples, from this last variable to translocation, and from translocation to fibre and leaf water.

Discussion

Nutritive value of young foliage

Foliar nitrogen of black booyong fell within the range of values reported for rainforest trees (e.g. Coley 1983; Janzen and Waterman 1984; Mattson and Scriber 1987) and for other evergreen trees such as Australian eucalypts (e.g. Fox and Macauley 1977; Ohmart et al. 1985). Likewise, leaf water and fibre were within the lower and upper bounds, respectively, of reported values from these hosts. The sharp decline in dietary quality of young leaves after the main leaf flush particularly affected psyllids and, along with a reduction *per se* in available young foliage, partly explained their lower abundance later in the season (Basset 1989). Hence, with the exception of the possible influence of chemical defences, the dietary quality of young black booyong leaves was higher than that of mature leaves and this difference was primarily due to higher levels of water and nitrogen, along with a lower specific leaf weight. Maturation of black booyong foliage was consistent with the leaf maturation processes reported for a wide range of host-plants (e.g. Mattson and Scriber 1987), although young leaves usually have much lower fibre content than mature leaves (e.g., Coley 1983; Janzen and Waterman 1984). Mooney and Gulmon (1982) attributed the positive relation between specific leaf weight and nitrogen of mature leaves to nitrogen dilution in maturing leaves: the longer the life span of the leaf, the higher the ratio of leaf weight to nitrogen. For black booyong, this ratio falls into the "tropical rain forest on laterite soil" category of Mooney and Gulmon (1982, Fig. 8). Overall, black booyong foliar characteristics appear similar to other rainforest trees, except for a tendency to be higher in fibre content and lower in water and nitrogen content; they are close in this respect to Australian eucalypts.

Predicting herbivore distribution in rainforest trees

The best predictor of herbivore abundance was the amount of young foliage, a result consistent with the resource concentration hypothesis of Root (1973). However, for certain herbivores, such as Chrysomelidae, dietary quality of foliage had little effect on insect abundance and distribution. Similarly, Strauss and Morrow (1988) observed that the field distribution of the chrysomelid *Chrysophtharta hectica* on its eucalypt hosts was influenced to a greater degree by the amount of nearby foliage of suitable age than to foliar nutrient content. The clumping of chrysomelids in the upper crown of *A. actinophyllum* was highlighted by correlations between abundance and variables such as the number of leaves within the samples (which is high in the upper canopy, where leaves are small) and air temperature. The biological significance of these observations remains uncertain, but may be related to preferences in highly illuminated foliage samples.

The results of this study assert the importance of foliar nitrogen, and particularly of translocation effects, in the spatial distribution of phytophagous insects associated with particularly nitrogen-poor rainforest trees. However, Wint (1983) stated that determinations of available leaf nitrogen (the total leaf nitrogen minus the amount of nitrogen rendered unavailable by leaf protein-complexing agents) are more relevant to herbivore growth and development than crude measurements of total leaf nitrogen. Furthermore, this author suggested that phloem-feeders are relatively unaffected by protein-complexing substances, since they extract their readily assimilable nitrogen directly from the vascular system, in which these defensive compounds are present as inactive soluble glucosides. Conversely, protein-complexing agents are located as active compounds in the cells of non-vascular tissues and their action is often pronounced in the digestive performance of chewing insects (Wint 1983). This difference in the feeding mode of chewing and sap-sucking species may explain the positive influence of translocation effects on sap-suckers (particularly psyllids) and the apparently weak effects on chewers. Translocation, which depends both on the magnitude of leaf production (Pate 1980) and on plant growth rate (Mooney and Gulmon 1982), has been shown to affect the distribution of aphids (Larsson 1985) and other sap-suckers, particularly psyllids (White 1984). Path analysis showed that leaf turnover significantly influenced the local availability of young foliage which, in turn, significantly affected translocation effects. Leaf turnover and nitrogen translocation are likely to be well-marked within the ecotone formed by the top layer of foliage in emergent rainforest trees, because illumination is not a limiting factor for leaf production within this layer. This fascinating arboreal habitat, which could not be adequately surveyed in the present study, certainly deserves further entomological investigation.

Among free-living herbivores associated with *A. actinophyllum,* the most specialized were psyllids feeding upon nitrogen-rich meristems, such as vegetative and floral buds. As seen previously, the distribution, and, presumably, the feeding responses, of generalist chewers and phloem-feeder specialists were different: the former were influenced primarily by the quantity *per se* of food items, while the latter were equally sensitive to the quality of their food items. Thus, setting aside chemical defences, rainforest evergreen tree species which disclose a relatively continuous leaf production (more "apparent" hosts *sensu* Feeny 1976) may also reveal a relatively high proportion of associated specialist chewers, in comparison with intermittently growing evergreens (less "apparent" hosts), such as *A. actinophyllum,* which may sustain more phloem-feeding specialists.

Leaf water, which usually limits nitrogen assimilation efficiency and nitrogen accumulation rate in chewing insects, is a factor of some importance in the spatial distribution of temperate herbivores (Scriber 1977). However, its significance in the present study was limited. Leaf water may not be limiting for rainforest herbivores during the wet season, since relative humidity and rainfall may be used as additional water sources. Furthermore, since foliar fibre was determined mostly from mature leaves, it is not certain whether this factor is important for herbivores feeding on young *A. actinophyllum* leaves. The effects of other chemical defences could not be investigated in this study and these may be considerable, depending on the extent of their diversity and variation in the young foliage.

Part of the fogging programme was designed to study the field distribution of arthropods in samples of varying leaf sizes and foliage compactness. In some instances, leaf size may be an important factor of leaf selection for herbivores, such as leaf-mining species (e.g. Bultman and Faeth 1986). In the present study, leaf size was not a consistent predictor of arthropod abundance on either young or mature foliage. Other sources of variation in herbivore abundance on rainforest trees, not mentioned previously, may include factors related to host colonization (e.g. local aerial currents, factors affecting locally insect activity, presence of conspecific trees within a certain distance), and factors related to foliage illumination. Crown openness was a crude measurement of this last variable. Precise and "long-term" estimation of the level of illumination within the samples would probably have been more useful for investigating the effects of this variable. The indirect effects of illumination may be high, since this factor can change drastically over a distance of a few metres inside a tree crown and may alter leaf production, foliar nutrients, foliar morphology, defence characteristics of leaves and insect activity (e.g. Mooney and Gulmon 1982; Harrison 1987; Moore et al. 1988). Although the data presented here do not allow further discussion of this point, it should be noted that the most illuminated tree, Tree 9, sustained high herbivore loads (particularly of chrysomelid beetles), although it did not have extremely high leaf turnover.

This simple field study raises a number of interesting questions concerning the influence of leaf production on the distribution of chewing and sap-sucking species respectively. Undoubtedly, studies of other rainforest hosts and their associated faunas are urgently required for adequate comparisons. Such studies are certain to yield numerous surprises for rainforest entomologists investigating insect-plant interactions, particularly due to the extreme diversification of rainforest trees and of their complex phenologies and chemical defences.

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