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Leaf production of an overstorey rainforest tree and its effects on the temporal distribution of associated insect herbivores

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Summary. The host phenology and temporal distribution of insect herbivores associated with a rainforest canopy tree, *Argyrodendron actinophyllum* (Sterculiaceae), were monitored for 3 and 2 years respectively in an Australian subtropical rain forest near Brisbane. Leaf production of this evergreen species was synchronous among individuals, occurring from October to February, but differed markedly between years for some fast-growing trees. Most herbivore species fed selectively upon young leaves and, consequently, occurred only during "windows" of young foliage availability, with the exception of some mesophyll-feeders that preferred mature foliage. Fast-growing trees sustained high herbivore activity during periods of intense leaf production but some slow-growing trees, whose availability of young foliage appeared to be more constant and predictable, also supported high herbivore activity in the long term. Host suitability of particular trees during study years was dependent upon the intensity of leaf production and other unidentified factors, and was different for generalist and specialist herbivores. Certain specialist species, such as psyllids, were able to overcome the changing availability of young foliage between years on vigorous *A. actinophyllum* trees by feeding upon both vegetative and reproductive meristems. Most of the data suggest that availability of young foliage is an important factor in this insect-plant system.

Key words: *Argyrodendron actinophyllum* – Insect-plant interactions – Insect temporal distribution – Plant phenology – Rain forest

A major determinant of the diversity of phytophagous insect communities is the seasonal development of the host-plant (Strong et al. 1984). Herbivores must not only locate a host-plant, but also find it within the period when tissues of appropriate age are available (Morrow 1984). These evolutionary and environmental constraints are likely to be considerable in rainforest environments, since high botanical diversity may limit herbivore dispersal and subsequent host colonization, and low nutrient availability of evergreen foliage (Mattson 1980) may impose severe restrictions on herbivore seasonality. There is abundant literature on the effects of leaf production on associated herbivores in temperate woodlands (review in Strong et al. 1984), but this topic has not been studied extensively in rainforest environments (e.g. Leigh and Smythe 1978; Coley 1982, 1986; Aide 1988; Aide and Londoño 1989; Ernest 1989). For example, there is no published information about the seasonal patterns of the entire herbivore community associated with a particular rainforest tree species. No doubt this paucity of data arises from difficulties in access and "long-term" insect sampling in the rainforest canopy. Often light traps have been operated to obtain data on seasonality of rainforest insects, but this methodology provides limited information on particular host-species, since trap effectiveness addresses only night-flying herbivores and trapping efficiency differs among insect taxa, sampling locations and lunar phases (Bowden 1982).

This study aimed to record herbivore activity within a particular rainforest canopy tree species with a technique minimizing some of the above problems. Herbivore temporal distribution was compared with observed patterns of host phenology. Although a wide range of arboreal arthropods was collected, the discussion is primarily restricted to active imagines (mostly day- and night-flyers) of the numerically important herbivore guilds feeding upon the host-tree studied (chewers, phloem- and mesophyll-feeders).

Field site and host-tree

The study was carried out in a stand of complex notophyll vine forest (warm subtropical rain forest), in the

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"Beauty Spot 54" of the Mount Glorious State Forest (27° 19′ 20″ S, 152° 44′ 55″ E, altitude 700 m), some 30 km NW of Brisbane, Queensland, Australia. The floristics of the site, whose canopy reaches 35–40 m, are detailed in Young (1985). Mean daily temperature approaches 18.0° C and mean annual rainfall amounts to 1658 mm. The Mt Glorious climate can be classified as "slightly seasonal humid", with a summer rainfall regime.

Argyrodendron actinophyllum (Bailey) Edlin, 1935, Sterculiaceae (Malvales) ("Black Booyong") is a tall evergreen and monoecious tree reaching up to 50 m. It is one of the dominant canopy species of the Australian warm subtropical rain forests and its main features include plank buttresses, scaly bark and palmate leaves. *A. actinophyllum* is a long-lived species of intermediate tolerance to shade. It is often referred to as a late secondary species, which may colonize the understorey of adjacent tall open forests of the wet sclerophyll type (P.A.R. Young pers. comm.). The biology and distribution of this rainforest tree are outlined in Boland et al. (1984).

Methods

Monitoring of host phenology

Ten mature Black Booyong trees (Trees 1–10) were climbed at weekly intervals with the single rope technique from February 1986 to February 1988 and then monthly until February 1989. Leaf production, expressed as percentage of young leaves present in the total foliage, flowering and seeding activity were visually estimated *in situ*. Secondly, litterfall traps of 60 cm × 60 cm were set up, at ground level, near the base of each study tree. Traps were emptied every 3 weeks from 1986 to 1988 and then monthly during the following year. The litterfall was sorted into the following categories: Black Booyong leaflets, flowers and seeds, other leaves, epiphytes and remaining litterfall (woody material, other flowers and fruits, etc.). This material was oven-dried at 100° C for 24 h and the dry weight was recorded for each category. Thirdly, stainless steel girth band dendrometers (see Hynes 1979) were secured upon the study trees 8 m above the ground at a height where buttresses do not distort the tree trunks. Cambial activity, as indicated by secondary girth increment, was measured concurrently with litterfall trap recordings. Air temperature was recorded simultaneously to allow correction for thermal expansion of the stainless steel tape (Hynes 1979). Crown openness (usually inversely proportional to the illumination of the crown) was determined using the photographic method of Walker et al. (1988).

Monitoring of herbivore activity

Five composite interception traps, consisting of malaise and window trap sub-units, were set up at the same height and orientation within the crowns of five out of the ten study trees (Trees 1–5). The collecting surface of each trap represented 0.5 m^2. Arthropods were collected continuously, day and night, and traps were surveyed at weekly intervals during 1986 and 1987 using the single-rope technique. Weekly maximum air temperatures were read from a maximum-minimum thermometer secured against the trunk next to each trap. Herbivore abundance was compared to herbivore activity on each study tree during a test-week in January 1987. Herbivore density was estimated by 8 samples of "restricted canopy fogging" (0.7 m^2 of leaf area enclosed within a plastic frame and fogged with CO_2), taken at different heights and locations within each tree crown. Sampling procedures and their limitations have been detailed, compared and discussed elsewhere (Basset 1988, 1989, 1990). The collected specimens were stored in 70% ethanol and sorted to families and morphospecies, which were examined subsequently by various taxonomists. The material was deposited at the Queensland Museum, Brisbane. The taxonomic composition of the arthropod community associated with *A. actinophyllum* has been analysed and a comprehensive checklist of species foraging within the crowns of this tree is available (Basset 1989, 1990, 1991a). In addition, herbivores were collected alive with modified interception traps and their feeding upon Black Booyong foliage was checked in glasshouse trials. The relative influence of temperature, rainfall and host phenology on the activity and seasonality of all arthropod guilds composing the Black Booyong arboreal community has been examined elsewhere (Basset 1991b).

Statistical methods

Temporal and spatial shifts in the herbivore community were investigated with detrended correspondence analyses of local occurrences in the traps (raw data) of the 36 most common herbivorous species. The ordinations were performed separately for 1986 and 1987. Since the first two axes of these ordinations accounted for more than 90% of the variance in herbivore activity in both cases (and were identically interpreted), the two ordinations could then be compared with a Procrustes rotation (Digby and Kempton 1987). The test matrix was chosen as the coordinates of the vectors in Axes I and II for 1986, while the 1987 ordination was chosen as the target matrix (overall fit between the test and target matrices: root mean square residual = 0.663). The interpretation of the Procrustes rotation was facilitated by computing stepwise multiple regression analyses. The dependent variables were the scores of trees for years 1986 and 1987, while independent variables included various phenological attributes determined during these years.

Herbivore activity was also expressed as percentage of total number of arthropods collected by traps. This procedure reduced the importance of annual changes in insect populations and the effects pertaining more specifically to tree and trap location (e.g. differences in illumination, relative humidity, aerial currents).

Results

Host phenology

The monitoring of ten trees (Fig. 1) plus casual observation of the tree population at Mt Glorious suggest that *A. actinophyllum* is a proleptic (i.e., flower development is discontinuous) and intermittently growing evergreen. Leaf production was synchronous among individuals (Kendall's coefficient of concordance for leaf production data, $W = 0.681$, Friedman's $\chi^2 = 748.7$, $df = 110$, $P < 0.001$), as were leaf fall (litterfall data, $W = 0.322$, $\chi^2 = 125.7$ $df = 39$, $P < 0.001$), reproductive activity (litterfall data, $W = 0.784$, $\chi^2 = 15.7$, $df = 39$) and secondary growth increment (dendrometer data, $W = 0.684$, $\chi^2 = 119.7$, $df = 35$, $P < 0.001$). Leaf flush occurred between October and February following leaf fall and its magnitude was significantly different among study years (Kruskal-Wallis' $H = 7.19$, $P < 0.05$). Flowering occurred between March and May, was profuse in 1986, barely noticeable in 1987 and absent in 1988. Cambial activity primarily occurred between December and February, after most of leaves had expanded. Net annual girth

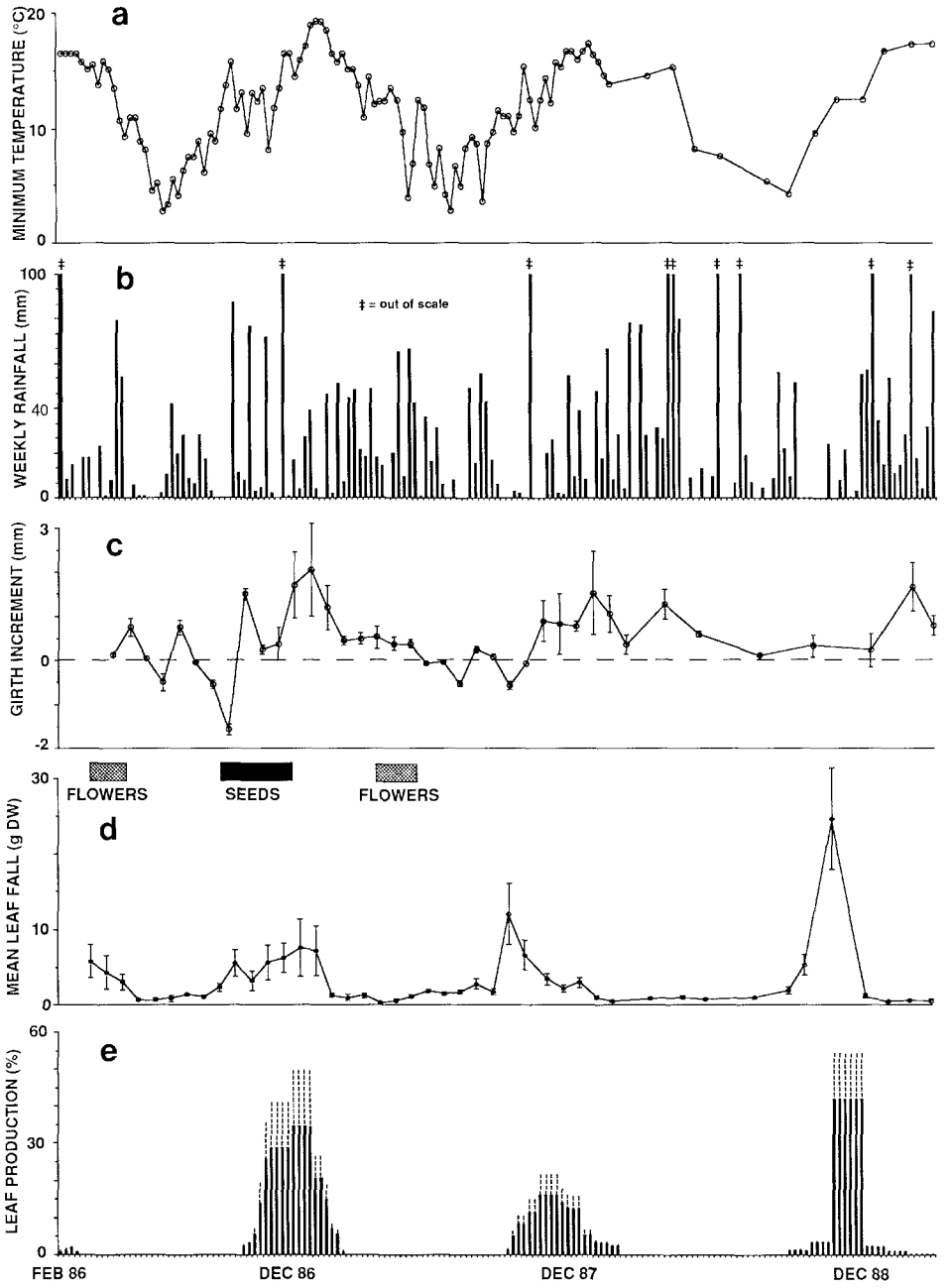

Fig. 1a–e. Abiotic factors and phenology of the ten study trees during 1986–1988 at Mt Glorious. **a** Weekly minimum temperature; **b** weekly rainfall; **c** mean secondary girth increment and reproductive activity; **d** mean leaf fall per trap for 21 day survey periods; **e** mean weekly percentage of young leaves (*vertical lines* and *broken lines* represent 1 SE)

increment was usually negatively correlated with annual foliage turnover, as defined by maximum leaf production ($r = -0.892$, $P < 0.05$, $df = 3$; $r = -0.710$, $P < 0.05$, $df = 8$; and $r = 0.399$, $P = 0.22$, $df = 8$; for 1986, 1987 and 1988, respectively). Figure 2 details the phenology of trees in which interception traps were secured. In the "long term" (3 years of observation), four out of the ten study trees could be classified as "fast growers", as indicated by their cambial activity (e.g. Trees 1 and 2 in Fig. 2). Net girth increment and reproductive activity were higher for these trees during the three study years. Their leaf production and secondary growth increment differed markedly between the study years. These last phenological events were more constant for "slow growers", such as Trees 4, 5, and to a lesser extent, Tree 3 (Fig. 2).

Herbivore temporal distribution

About 8,500 insect herbivores were collected by the five traps during the two study years. Correlation between herbivore activity and herbivore abundance was highly significant during the test-week (Fig. 3). Fogging samples from other trees showed that increase in herbivore activity was generally correlated with actual changes in herbivore density (Basset 1990, 1991b). Most (76%) of herbivores were intercepted during "windows of availability" of young foliage (Fig. 4). Chrysomelids and scarabaeids were only found during leaf-flush periods, whereas some cicadellids were also active later in the season. In fact, some mesophyll-feeders (e.g. most Typhlocybinae and Thysanoptera) preferred to feed upon mature

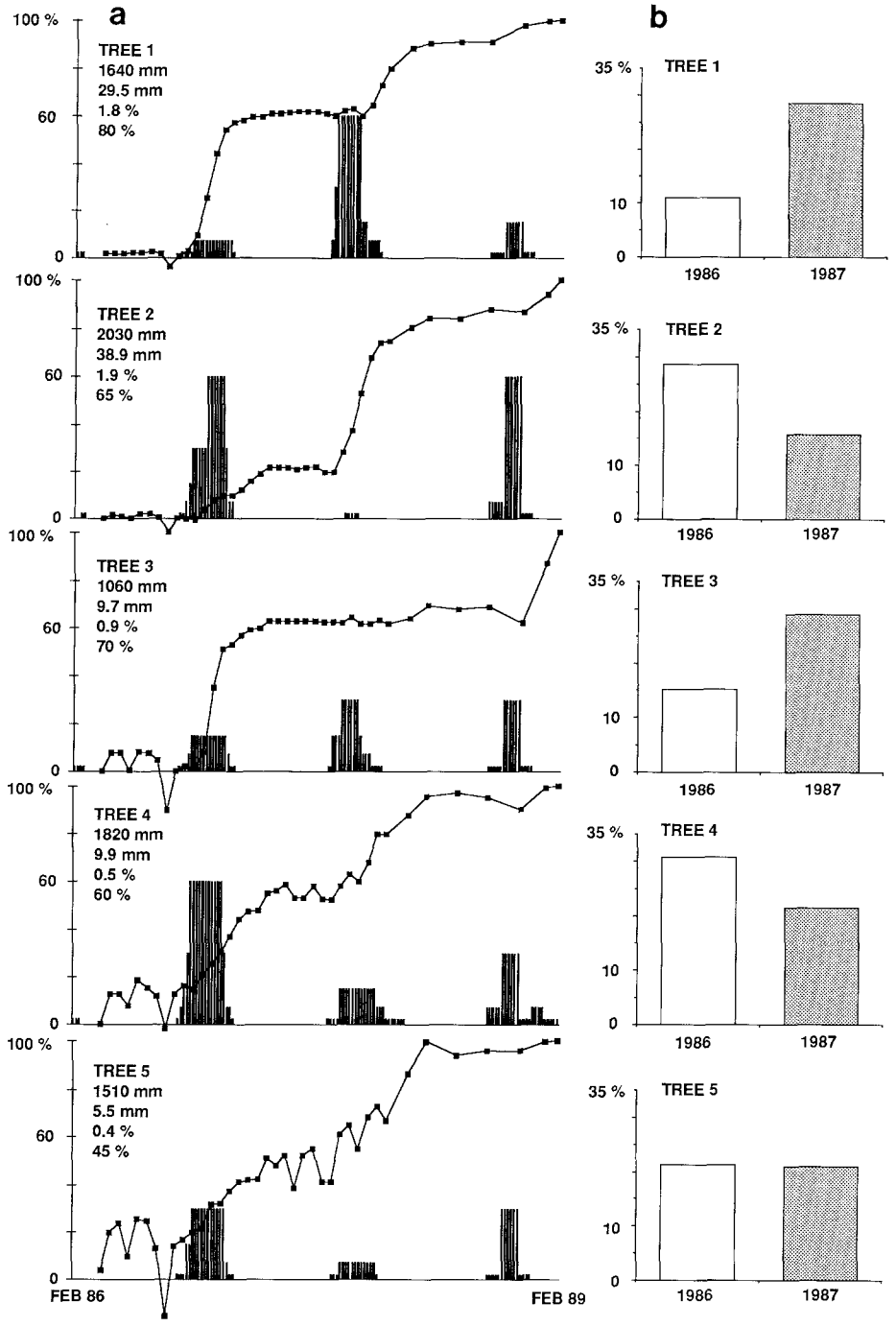

Fig. 2a, b. Phenology of Trees 1–5 and corresponding herbivore activity. **a** Leaf production (*bars*) and cumulative percentage of girth increment (*curve*) during 1986–1988 (with initial girth, total increment at the end of the study, % increment of initial girth and crown openess for each tree); **b** percentage of herbivores collected in interception traps during 1986 and 1987

leaves and were spatially restricted to this leaf cohort (Basset 1991b). Psyllids fed also on flowers, particularly during March – May 1986, a year of high reproductive activity for Black Booyong.

Foliar nitrogen and water content were higher in young *A. actinophyllum* leaves than in mature leaves (e.g. nitrogen: average 1.80 and 1.62% DW, respectively, $t=2.43$, $P<0.05$, $df=193$, see Basset 1991c). Glasshouse trials indicated that the commonest herbivores collected in this study feed only on young leaves (all Chrysomelidae, Curculionidae and Lepidoptera tested, some Cicadellidae and Psylloidea; 27 species tested; see details in Basset 1989). Henceforth, this paper focuses on herbivore-tree interactions during host leaf flush periods.

The proportion of herbivores to the total number of arthropods collected in the traps was significantly non-uniform between study trees and between study years (Table 1). Trees exhibiting intense leaf production sustained high herbivore activity (Table 1), particularly when this was expressed as the proportion of total catches (Fig. 2b; Trees 4 and 2 in 1986; Trees 1 and 3 in 1987). Differences in herbivore activity during the two study years were evident, particularly for Trees 1, 2 and 3, and, for these trees, were related to the intensity of foliage

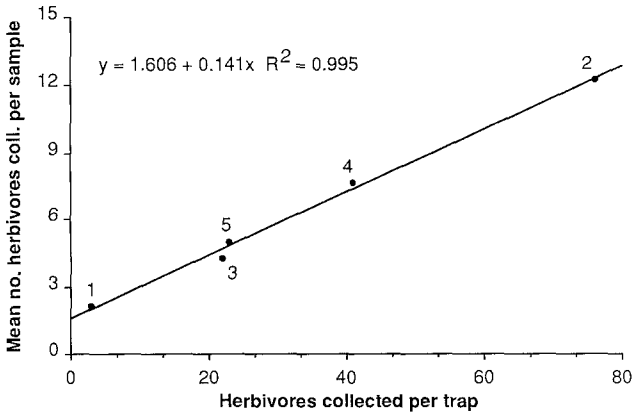

Fig. 3. Correlation between the mean number of herbivores collected per fogging sample ($n=8$) on each study tree, and the number of herbivores collected by corresponding traps during the test-week (15–22 January 1987). *Numbers* refer to trees

turnover. The proportion of herbivores collected was also non-uniform between trees at the end of the two-year study ($G=46.8$, $P<0.001$), but this was so because of the high proportion of herbivores on Tree 4 (herbivore proportions = 20.1%, 22.8%, 22.1%, 26.9% and 21.1% for Trees 1–5, respectively).

The plot of the Procrustes rotation is detailed in Fig. 5. For the sake of clarity, some taxa that should have been plotted in the center of the figure have been omitted. The first axis of the ordinations accounted for 63.5% and 74.5% of the variance in herbivore activity in 1986 and 1987, respectively. The intensity of leaf production partly contributed to the formation of this axis, but it was clearly not the only causal factor (correlation between tree scores on Axis I and annual leaf turnover: $r=0.354$, n.s.). The scores of the trees were better explained by a variable defined as the annual sum of weekly leaf production (as seen in Fig. 2) multiplied by the annual girth increment, expressed as percentage of initial girth ($r=0.701$, $P<0.05$; Table 2). The number of non-herbivores collected entered second in the stepwise regression analysis (Table 2), suggesting that the formation of Axis I was also determined by non-phenological parameters. Axis I further segregated relatively specialized herbivores in the right-hand side of Fig. 5 (e.g. psyllid nymphs, *Aconopsylla* sp.) from generalist herbivores in the left section (e.g. *Cotylana angustifrons, Longitarsus* sp., Genus nr *Callinesia;* see details in Basset 1989). Thus, on the basis of these various observations, Axis I was interpreted as a measure of host suitability for herbivorous insects. Host suitability was interpreted as being at a minimum in the left-hand section of the ordination, then increases for generalist herbivores in the centre, and reaches maximum values for specialist taxa in the right section of the ordination.

The second axis of the ordinations accounted for 29.8% and 16.8% of the variance in 1986 and 1987, respectively. The scores of the trees on this axis could be explained statistically (Table 2), but the biological interpretation was not straightforward. The best descriptors included, firstly, a variable defined as the sum of weekly maximum temperatures recorded during the peak-time of leaf production divided by crown openness ($r=0.659$, $P<0.05$), and, secondly, initial tree girth. However, Axis

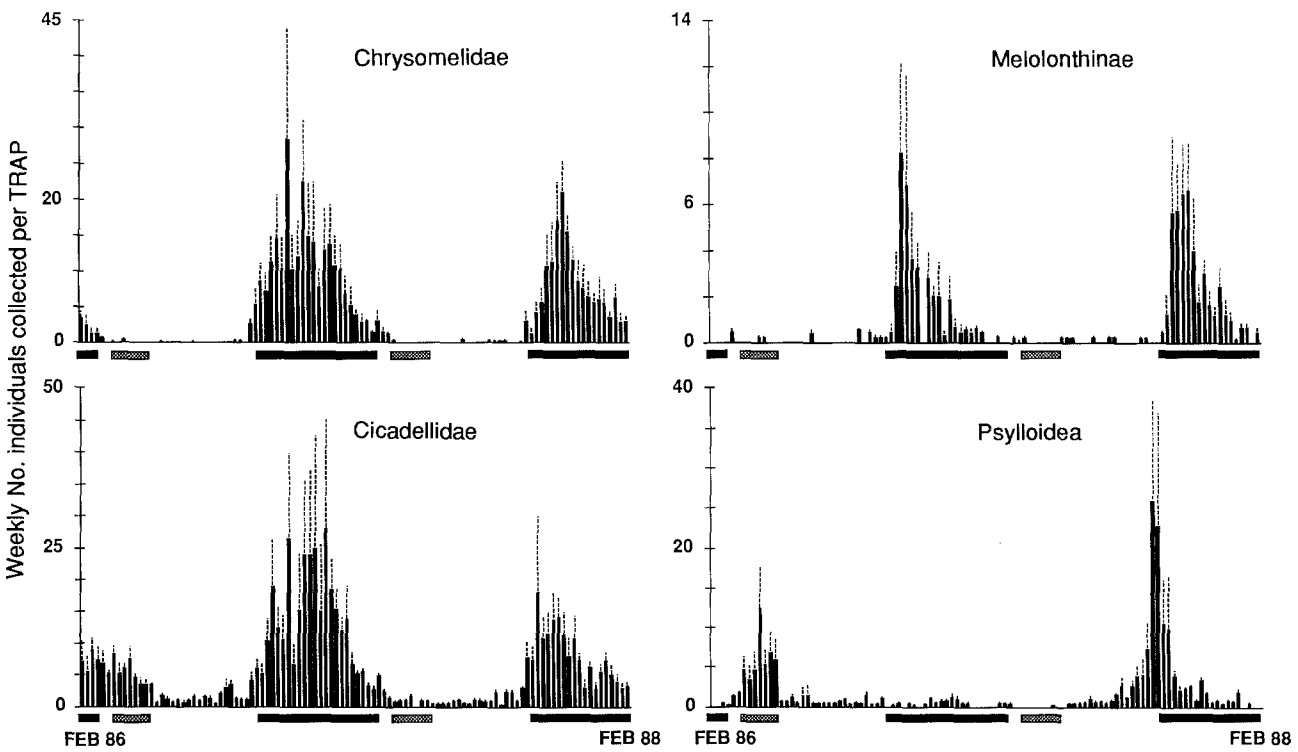

Fig. 4. Temporal distribution of selected herbivore taxa. Plot of weekly number of individuals collected per trap (*solid bars* represent means, *broken lines* 1 SE), with respect to host leaf flush (*horizontal black bars*) and host flowering (*horizontal grey bars*)

Table 1. Total number of herbivores collected in interception traps during the leaf flush periods of 1986 (first line) and 1987 (second line), and *G*-tests of uniformity between trees and between years

Taxa/Guild	Tree 1	Tree 2	Tree 3	Tree 4	Tree 5	*G*, Trees [1]	*G*, Years
All arthropods	2227	5156	3002	3043	1663	–	136.6***
	2431	4263	2948	2178	1516	–	
All herbivores	245	1477	459	940	355	333.3***	784.4***
	692	670	856	467	317	153.2***	
All chewers	62	478	198	502	110	290.8***	255.6***
	183	269	305	186	95	38.7***	
All phloem-feeders	171	960	220	374	179	232.6***	563.7***
	486	376	502	233	185	163.3***	
All mesophyll-feeders	12	41	41	64	66	90.5***	14.4**
	23	25	49	48	37	48.6***	
Chrysomelidae	52	447	175	390	70	236.1***	145.9***
	85	249	242	129	71	52.6***	
Melolonthinae	6	18	14	109	37	186.8***	136.6***
	89	13	52	50	18	120.3***	
Cicadellidae	127	767	206	249	136	185.7***	342.2***
	137	172	345	102	103	149.8***	
Psylloidea	3	13	8	8	13	12.1*	61.6***
	298	32	102	91	39	425.4***	
Lepidoptera-caterpillars	3	7	7	1	2	5.2 n.s.	2.8 n.s.
	6	7	7	5	3	0.8 n.s.	

[1] Comparison with total no. arthropods collected the corresponding year
* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$, n.s. not significant

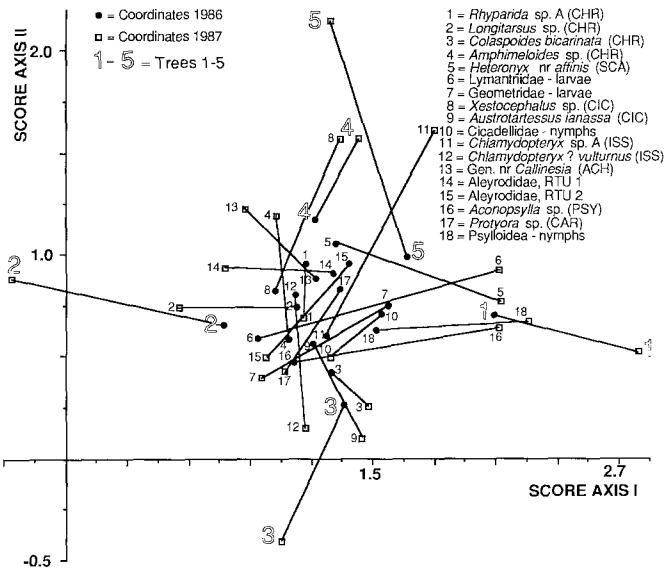

Fig. 5. Procrustes rotation of detrended correspondence analyses of herbivore activity within five Black Booyong trees during 1986 and 1987 (*CHR* = Chrysomelidae, *SCA* = Scarabaeidae, *CIC* = Cicadellidae, *ISS* = Issidae, *ACH* = Achilidae, *PSY* = Psyllidae, *CAR* = Carsidaridae, *RTU* = recognizable taxonomic unit)

II segregated taxa occurring early during the leaf flush period from those active later in the season (upper and lower parts of Fig. 5, respectively). A weak correlation existed between insect scores and the week of highest insect occurrence ($r = -0.378$, $P < 0.05$). The number of herbivores collected per trap during a particular year was best explained by annual foliage turnover and the sum of weekly maximum temperatures during leaf flush, while the corresponding percentage data were only dependent upon annual foliage turnover (Table 2).

Discussion

Replication of long-term insect sampling in the rainforest canopy (in contrast with short-term sampling with canopy fogging, for example) is time- and labour-consuming. Consequently, the restricted number of trees examined impairs the scope of the present discussion. Furthermore, it is well-known that no ideal insect-sampling device exists and that every method is biased towards certain groups and/or environmental factors (e.g. Basset 1988). Although there was a good correlation between herbivore abundance and herbivore activity during the test-week, this was not necessarily so in the other 103 weeks of the sampling programme. Herbivore activity may be influenced by air temperature, rainfall, relative humidity, illumination, moon phase, characteristics of the foliage in the vicinity of the trap, presence of conspecific hosts, aerial currents, etc (Basset 1991b), and, of course, by annual changes in insect populations (Wolda 1978). For example, there is strong suspicion that Axis I of the Procrustes rotation may be related to herbivore abundance, whereas Axis II may be more dependent upon herbivore activity (see below).

The information presented in this study suggests that most herbivores feeding upon *A. actinophyllum* are dependent upon young foliage availability. However, as

Table 2. Summary of stepwise multiple regression analyses performed with dependent variables determined in 1986 and 1987

Dependent variable	Variable entered	R^2
Scores of trees on Axis 1		
Step 1	annual Σ of weekly leaf production × percentage annual girth-increment	0.49
Step 2	annual no. of non-herbivores collected	0.86
Final equation $y = 2.059 + 0.006x_1 - 0.001x_2$ [1]F-test = 22.3***		
Scores of trees on Axix 2		
Step 1	annual Σ of weekly maximum temperatures during leaf flush × crown openess^{-1}	0.43
Step 2	initial tree girth (mm)	0.78
Final equation $-2.070 + 0.191x_1 + 0.001x_2$ [2]F-test = 12.2**		
No. herbivores collected		
Step 1	annual foliage turnover	0.52
Step 2	annual Σ of weekly maximum temperatures during leaf flush	0.77
Final equation $y = 886.174 + 9.255x_1 - 1.706x_2$ [2]F-test = 11.8**		
% herbivores collected		
Step 1	annual foliage turnover	0.72
Final equation $15.138 + 0.248x_1$ [1]F-test = 20.3**		

[1] All parameter estimates with $P < 0.01$ [2] All parameters estimates with $P < 0.05$
** $P \leq 0.01$, ***$P \leq 0.01$

exemplified by some mesophyll-feeders, this was not true for all insect groups. Similarly, in Britain, most canopy Typhlocybinae feed upon mature leaves both during nymphal and adult stages (Claridge and Wilson 1976).

Energy-demanding phenological events, such as leaf flush, flowering and fruiting, are often associated with times of lesser girth increment in rainforest trees (Hazlett 1987). The segregation observed in the growth pattern of the study trees (slow and fast growers) is unlikely to be accounted for by differences in tree age alone, since some slow growers were situated in "juvenile" (young regrowth) patches of rain forest. Rather, slow growers are interpreted as being less vigorous and more stressed trees than fast growers. Coley (1986) showed that for the rainforest tree *Cecropia peltata* there exist intra-specific trade-offs between growth, reproduction and defence. The level of defences and nutrients in the foliage of Trees 1 to 5 were not investigated during the study years. Webb (1952) did not find any trace of alkaloids in *A. actinophyllum* leaves, but this species often produces gum. Tannins, which are particularly abundant in Sterculiaceae (Hegnauer 1973), and other polyphenols, may also be present in the foliage. Black Booyong, whose foliage is characterized by low nitrogen and water content, high fibre content and absence of alkaloids, probably falls into the category of rainforest trees which are protected by dose-dependent "quantitative defences" (Feeny 1976; Waterman and McKey 1989). Therefore, it is probable that the level of chemical defences may differ between fast- and slow-growing *A. actinophyllum* and that the level to which their foliage is defended may also differ between years.

The scores of trees on the first axis of the Procrustes rotation were best explained by a variable accounting for both annual leaf turnover and annual girth increment. This suggests that host suitability is probably determined by a complex set of interactions between the intensity of leaf production and the balance between foliage defences and nutrients, which may be related to tree growth. However, Axis I was also explained by a variable not directly related to phenological events, the number of non-herbivores collected in the traps. Dethier (1988) proposed an extended definition of host suitability and stated that this concept is related to food availability, absence of toxicity, the probability of finding an adequate number of host-plants within some critical time, and the effectiveness of the plant as shelter. This last point may be important for specialist herbivores feeding upon *A. actinophyllum*. For example, increased leaf production may influence the architectural complexity of the host, and may alter the foraging strategies of predators and parasitoids. Although alternative explanations relevant more specifically to trap efficiency cannot be totally discounted, it is probable that local aerial currents, tree location (e.g. next to clearings and/or close to conspecifics) and local activity of predators and parasitoids are important parameters in defining host suitability. These factors are probably important for specialist species, which may be involved in more "active" process of host colonization, than generalist species.

This argument would in part explain the segregation between generalist and specialist species on Axis I. It is well recognized that specialists are very sensitive to the abundance of their food plants (e.g. Root 1973; Fox and Morrow 1981). For example, Rockwood (1974) documented shifts towards trees of improved foliage (hand-defoliated trees which were stimulated to produce extensive batches of young leaves) by a specialist chrysomelid beetle on its Costa Rican host-tree. Usually, species that are highly intimate with their hosts (gall-formers, miners, sap-feeders) exhibit much greater tree-to-tree differences in population and injury levels than do less intimate

species (free-living folivores) (Mattson et al. 1988). As exemplified by *A. actinophyllum*, the actual level of host suitability may differ for generalist and specialist herbivores. Escape of the host in space and time from specialist herbivores is common, as investments in defensive chemistry for protection from specialists are comparatively higher than the investments required for protection from generalists (Krischik and Denno 1983). For example, specialists may overcome the changing leaf-production of host by attacking different tissues of high nitrogen content, particularly if the availability of these food resources are little or negatively correlated between years. *Aconopsylla* sp. and *Protyora* sp., psyllids which are amongst the most specialized of the Black Booyong herbivores, present such feeding behavior and damage both flowers and young leaves. Thus, their pattern of occurrence on individual trees is further complicated by the reproductive activity of their hosts.

The biological interpretation of Axis II, which explained between 15 and 30% of the variance in herbivore activity, was not straightforward. Neither indirect measurements of crown illumination (crown openness) nor synchronism between peak time of leaf production and maximum air temperatures could directly explain it. Furthermore, the timing of bud break and of peak leaf production, and the duration of the period over which young foliage was available did not unequivocally contribute to it. No parameters potentially able to influence locally trap efficiency, such as air temperature, relative humidity, or denseness of the foliage in the vicinity of the trap, had any influence in this regard. However, the segregation of early- and late-flyers in the upper and lower part of the Procrustes rotation suggests that Axis II may be more dependent upon insect activity than upon actual insect abundance.

When herbivore activity was expressed as a percentage of total number of arthropods collected by traps, the tree sustaining the highest herbivore activity during the 2-year study was Tree 4. This slow-growing tree exhibited a relatively predictable leaf production and appeared to be the most "stable" tree during study years (Fig. 5: reduced shifts on both axes). Another slow-growing tree (Tree 10), investigated by restricted canopy fogging, showed a similar and predictable leaf production and high herbivore loads (Basset 1991c). Slow-growing trees are expected to be better defended than fast-growing ones (Coley et al. 1985). However, any increase in tree apparency may be particularly important for rainforest herbivores, since their hosts are non-apparent most of the time (Feeny 1976). For herbivores associated with rainforest trees particularly low in foliar nutrients, such as *A. actinophyllum*, this factor may even be more important in the long-term than small and short-term differences in the level of quantitative defences. This supposition will need rigorous testing and evaluation.

Undoubtedly, this simple field study raised many questions about the influence of the phenology of rainforest trees on the activity of associated herbivores. Long-term monitoring of host-trees and associated herbivores in different insect-plant systems, and careful field experimentation, appear to be imperative for a proper understanding of insect-plant interactions in rain forests.

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