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Communities of insect herbivores foraging on saplings versus mature trees of *Pourouma bicolor* (Cecropiaceae) in Panama

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Abstract The arthropod fauna of 25 saplings and of three conspecific mature trees of *Pourouma bicolor* (Cecropiaceae) was surveyed for 12 months in a tropical wet forest in Panama, with particular reference to insect herbivores. A construction crane erected at the study site provided access to tree foliage in the upper canopy. A similar area of foliage (ca. 370 m²) was surveyed from both saplings and trees, but samples obtained from the latter included 3 times as much young foliage as from the former. Arthropods, including herbivores and leaf-chewing insects with a proven ability to feed on the foliage of *P. bicolor* were 1.6, 2.5 and 2.9 times as abundant on the foliage of trees as on that of saplings. The species richness of herbivores and proven chewers were 1.5 ($n=145$ species) and 3.5 ($n=21$) times higher on trees than on saplings, respectively. Many herbivore species preferred or were restricted to one or other of the host stages. Host stage and young foliage area in the samples explained 52% of the explained variance in the spatial distribution of herbivore species. Pseudo-replication in the two sampling universes, the saplings and trees studied, most likely decreased the magnitude of differences apparent between host stages in this forest. The higher availability of food resources, such as young foliage, in the canopy than in the understorey, perhaps combined with other factors such as resource quality and enemy-free space, may generate complex gradients of abundance and species richness of insect herbivores in wet closed tropical forests.

Keywords Species richness · Rainforest · Understorey · Upper canopy

Introduction

Insect herbivores in temperate forests rarely show clear patterns of vertical stratification within host plants and, usually, no distinct insect communities can be recognized between host stages or forest strata (e.g. Fowler 1985; Schowalter and Ganio 1998; Le Corff and Marquis 1999). In tropical rainforests, many abiotic and biotic characteristics of the upper canopy (the uppermost leaf layer) are different from those of lower forest layers. Illumination, air temperature, wind, fluctuation of relative humidity and water condensation at night are notably higher in the upper canopy than in the understorey (e.g. Blanc 1990; Parker 1995). The foliage of mature trees is likely to be affected by a different microclimate than that prevailing in the understorey. This may have important implications for the foraging strategies of insects which can be affected profoundly by light regime and microclimate (e.g. Roubik 1993).

Usually, leaf area density and the abundance of young leaves, flowers and seeds are higher in the upper canopy than below (e.g. Parker 1995). Insect species richness in tropical rainforests is constrained by several historical and ecological factors. For leaf-feeding insects, the availability and predictability of young foliage is crucial (e.g. Strong 1977; Basset 1996). Many studies of rainforest insects have reported a higher abundance, activity or diversity of insect herbivores in the upper canopy than in the understorey (e.g. Sutton 1983; Basset et al. 1992). However, these studies compared whole forest strata, rather than comparing the specific resources available to insect herbivores in these strata. A rigorous way of studying these vertical gradients may be to compare insect herbivores that feed on conspecific seedlings, saplings and mature trees, particularly if the latter reach the upper canopy.

With few exceptions (Basset et al. 1999), this approach has focused mainly on leaf damage (e.g. Macedo and Langenheim 1989; Barone 2000). Such data may help botanists to understand patterns of attack on seedlings in tropical rainforests, perhaps as a result of insect dispersal or contagion from parent trees (e.g. Janzen

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1970; Leigh 1994). However, studies of insect stratification may be crucial toward understanding the distribution and maintenance of biodiversity in tropical and temperate forests. Several popular hypotheses involving concepts such as tree architecture (Lawton 1983), resource concentration (Root 1973) or resource base (Price 1992), along with the effect of abiotic factors, could explain vertical gradients of insect diversity in tropical rainforests. Most likely, these explanations are not mutually self-exclusive. The objectives of this study were to compare the herbivore fauna foraging on saplings and mature trees of one plant species in a tropical wet lowland rainforest in Panama and to test whether putative differences were related to simple measurements of availability of food resources.

Materials and methods

Study site and plants

The study site was at the Fort Sherman Canopy Crane, in the San Lorenzo Protected Area, Colon Province, Panama (9°17'N, 79°58'W, ca. 150 m a.s.l.). It is located in an approximately 200-year-old lowland wet rainforest receiving 2,700–3,000 mm of annual rainfall, with an average annual temperature of 25.2°C at Ga-

tun Locks, 5.5 km away from the site (Condit 1998; S. Paton, personal communication; Panama Canal Authority). The site has not been intensively logged for at least 200 years and 228 species of trees and shrubs with diameter at breast height (DBH) ≥ 1 cm have been recorded from a 6-ha plot there (S. Lao, personal communication; Condit 1998). Although the site is relatively flat, steep slopes may occur in some gullies. Access to the upper canopy was provided by a construction crane, 55 m tall with an arm reach of 54 m, erected within the 6-ha plot (Wright and Colley 1996). The maximum canopy height was ca. 40 m. A crane operator controlled the position of the crane gondola, from which insect collections were performed. The system provided good canopy access to at least 67 plant species within the arm reach of the crane (M. Samaniego and E. Charles, personal communication).

More than 30 species of *Pourouma* (Cecropiaceae) are known from southern Mexico to Brazil (Woodson and Schery 1960). *Pourouma bicolor* Martius is a pioneer species from lowland rainforests (Woodson and Schery 1960; Kobe 1999). It is common at the study site, where about 140 specimens with DBH ≥ 1 cm have been censused on the 6-ha plot (S. Lao, personal communication). It exhibits continuous leaf-flushing and stem growth throughout the year (Frankie et al. 1974). Its mature leaves are large (864 ± 77 cm², $n=72$ upper canopy and understorey leaves; one-sided area), with a tomentous pubescence underneath and appear tougher in the upper canopy than in the understorey. Three mature *P. bicolor* trees 17 m (1C), 30 m (2C) and 27 m tall (3C) were reachable by the crane. Most samples obtained from these trees originated from the upper canopy. Twenty-five saplings of *P. bicolor*, all smaller than 4 m, were studied on the 6-ha plot (Table 1). They represented about 90% of the sapling population present within the plot.

Table 1 Main characteristics of the study plants. 1C, 2C and 3C are mature trees, the remainder are saplings of *Pourouma bicolor*. The plant codes are those used in the ordinations. DBH Diameter at breast height; Openness % of canopy openness; Area estimated leaf area, measured at the initiation and end of the study for sap-

lings; Area young average leaf area of young foliage surveyed per sample; CV coefficient of variation of leaf production during surveys 1–25; No. of conspec. number of conspecific plants with DBH ≥ 1 cm within a radius of 50 m

Plant code	DBH (mm)	Openness (%)	Area (m ²)		Area (cm ²)	CV	No. of conspec.	No. of samples
			September 1998	September 1999	Young			
1C	132	37	–	55	214.0	0.63	6	200
2C	492	97	–	100	212.6	0.42	10	665
3C	450	78	–	140	179.4	0.48	8	175
1	16	5	1.1	3.1	42.2	1.32	8	75
2	24	9	0.7	1.7	20.3	3.76	9	25
3	11	5	0.3	0.6	32.3	2.60	6	25
4	17	4	0.2	0.4	24.0	2.34	14	25
5	9	3	0.1	0.1	0	–	16	22
6	17	4	1.7	1.5	27.3	2.34	17	53
7	13	34	1.1	2.3	53.7	1.06	22	75
8	10	4	0.2	0.8	128.0	3.57	19	25
9	13	13	0.8	0.9	165.7	2.70	18	49
10	12	7	0.6	0.9	55.0	2.21	19	25
11	19	4	0.4	0.5	85.9	5.00	28	25
14	13	11	0.3	0.5	91.0	1.50	16	24
15	15	7	0.9	0.8	99.6	1.51	17	26
16	19	6	0.7	1.9	31.0	2.13	13	51
18	14	6	1.3	0.9	51.6	1.25	7	51
22	25	10	1.9	4.0	152.4	3.09	20	75
23	18	8	1.0	1.7	61.1	1.38	24	51
24	13	4	0.7	0.5	49.0	2.46	3	25
25	19	11	0.6	0.7	92.4	1.21	16	26
26	40	20	3.8	3.8	0	–	4	18
28	20	25	0.8	2.0	103.2	2.45	3	50
29	21	24	4.6	3.2	36.2	1.25	3	99
31	8	10	0.7	1.0	121.8	1.97	40	49
32	10	9	0.4	1.1	88.1	1.76	40	19
34	10	8	0.6	1.3	188.3	1.20	29	13

Measurement of sample size

The sampling procedure was intended to survey a similar amount of leaf area on saplings and mature trees, in order to compare directly insect variables between host stages. First, the area of 72 leaves obtained from different trees and saplings on the study site were measured with a leaf area meter. Three leaf categories were recognized, irrespective of host stage: small (leaf area ≤ 500 cm²), medium-sized ($500 < \text{area} \leq 1,000$ cm²) and large ($\text{area} > 1,000$ cm²). These categories were used as a visual guide to determine a sample size close to 0.35 m² of leaf area. Young leaves were assigned to half of the area of small mature leaves. Final sample size was estimated by recording the leaves in different categories that were effectively surveyed and multiplying them by the average leaf size measured for each leaf-size category in each of the four above situations. Eventually, average sample size obtained from saplings and trees proved to be 0.353 ± 0.002 m² and 0.376 ± 0.004 m² of leaf area, respectively. This difference in sample size was consistent (Mann-Whitney $U=409,757.0$, $P<0.001$) but small (7%). It was assumed to affect negligibly insect variables, which were not corrected accordingly. This point is further addressed in the Discussion.

Insect collecting and processing

The study targeted free-living insect herbivores (leaf-chewing and sap-sucking insects). Using the crane gondola, arthropods were collected with a square beating sheet of 0.397 m² area, of conical shape (slopes of 45°), ending in a circular aperture (7 cm diameter), which was fitted with a removable plastic bag. Arthropods were dislodged from a putative sample size of 0.35 m² of leaf area (as described above) with three firm blows, and brushed gently into the plastic bag, which was then closed and replaced by a new one. The leaves beaten were then inspected carefully to discover any remaining arthropods, and these were collected as part of the sample. Insects that flew away during the beating procedure were recorded and assigned to family level. Flowers and fruits were avoided in the samples in order to remove the variance between saplings and trees due to the presence of reproductive structures.

Eighty such samples were collected during one survey, 40 each on saplings and trees. Twenty-five surveys were completed from November 1998 to October 1999. A survey for either saplings or trees was performed within a day and the other host stage was usually surveyed 2–4 days later. Samples were distributed among saplings and trees as indicated in Table 1. Some saplings were not used throughout the study and were replaced by others. In total, 1,000 samples were collected from each host stage. Samples were collected during the day, usually from 0900 hours to 1400 hours. A supplementary survey in October 1999 was performed during the night (2100–2400 hours). This survey indicated very few differences in the composition and abundance of the fauna in comparison with that collected during day.

Live leaf-chewing insects collected in the field were stored in plastic vials at room temperature, provided with young foliage of *P. bicolor*, and kept until they fed or died. Specimens feeding were assigned to the “feeding” category (“proven feeders” in the text), others to the “not feeding” category. Usually, conspecific insects consistently accepted or rejected the foliage of *P. bicolor*. Arthropods were counted, sorted to familial or higher taxonomic level, and assigned to arboreal guilds: leaf-chewers, sap-suckers, pollinators, epiphyte grazers, fungal-feeders, insect predators, other predators, parasitoids, wood-eaters, scavengers, ants, tourists and unknown (Moran and Southwood 1982). Adults of insect herbivores (s.l.: leaf-chewing, sap-sucking and wood-eating insects) were dry-mounted, sorted by morphospecies (hereafter “species” for the sake of simplicity), identified with a code and issued an individual voucher label. Arthropod data were managed using the software Biota (Colwell 1997a) and the material was deposited at the University of Panamá.

Statistical methods

Since raw data were non-normal, differences between saplings and trees were examined with Mann-Whitney tests. These tests were applied to the most common guilds, higher taxa and species collected (total number of individuals collected ≥ 15 or ≥ 100 for species and higher taxa, respectively). To account for the multiplicity of tests performed, Bonferroni's corrections were applied. The Chao1 statistic was calculated to estimate the total number of herbivore species likely to be present on both host stages (e.g. Colwell and Coddington 1994). The rarefied number of species present in a sample of n individuals was computed with Coleman's curve (e.g. Colwell and Coddington 1994), whereas the evenness of communities on both host stages was estimated with the index of evenness (E), proposed by Bulla (1994). Similarities in herbivore communities were calculated with the Morisita-Horn index (Magurran 1988). The Chao1, Coleman and Morisita-Horn statistics were calculated with 50 randomizations computed by the programme EstimateS (Colwell 1997b). Differences in the structure of communities on both host stages were tested further between pairs of species-abundance distributions (species ranked by abundance) with the Kolmogorov-Smirnov two-sample test (Tokeshi 1993).

Detrended correspondence analyses (DCA) and canonical correspondence analyses (CCA) were performed with the programme CANOCO (Ter Braak and Smilauer 1998) to evaluate the effects of host stage on the spatial distribution of herbivore species. Analyses were performed with herbivore species collected with six or more individuals (the first quartile of the species distribution ranked by abundance; 55 species: 16 chewers, 14 sap-suckers and 25 wood-eaters). Samples were pooled among study plants (25 saplings and three trees), emphasizing individual plants as the source of variation. Partialling out the total variance in the system from that accounted by the variables measured followed Borcard et al. (1992). The following independent variables (Table 1) were used for each study plant in the CCA:

1. A dummy variable accounting for host stage (saplings=1, trees=2).
2. The DBH of the study plant.
3. The canopy openness above the plant as estimated with a spherical densiometer (Model-A; Forest Densimeters, Bartlesville, Okla.), on 30 September 1999. Measurements for trees included the average of three readings in different positions, while a unique measurement was recorded for saplings.
4. The total area of mature foliage present on the study plant at the end of the study, estimated by counting the number of leaves and multiplying this figure by the average leaf area. For trees, leaf counts were approximate but are still informative for the estimation of the magnitude of difference between study plants.
5. The average area of young foliage surveyed per sample.
6. The coefficient of variation of leaf production (sum of young leaf area surveyed per survey) during all surveys.
7. Number of conspecific plants (DBH ≥ 1 cm) within a radius of 50 m of the study plant.
8. The number of samples obtained from each study plant, accounting for sampling effort.

Results

In total, 376.0 m² and 366.7 m² of foliage, including 7.0 m² and 21.5 m² of young foliage, were surveyed from saplings and trees, respectively. Young foliage was present on saplings and trees during all surveys, and was, on average, 3 times more abundant on trees than on saplings (Mann-Whitney $U=265,350$, $P<0.0001$). On average 4.210 ± 0.156 arthropods were collected per sample (total 8,590), which included 0.364 ± 0.002 m² of leaf area. This material includ-

ed on average 0.270 ± 0.019 and 1.242 ± 0.112 leaf-chewing and sap-sucking insects per sample, respectively (total 3,084 insect herbivores). Arthropods were about 1.6 times as abundant on the foliage of trees as on that of saplings (averages 5.180 ± 0.268 and 3.203 ± 0.148 per sample, re-

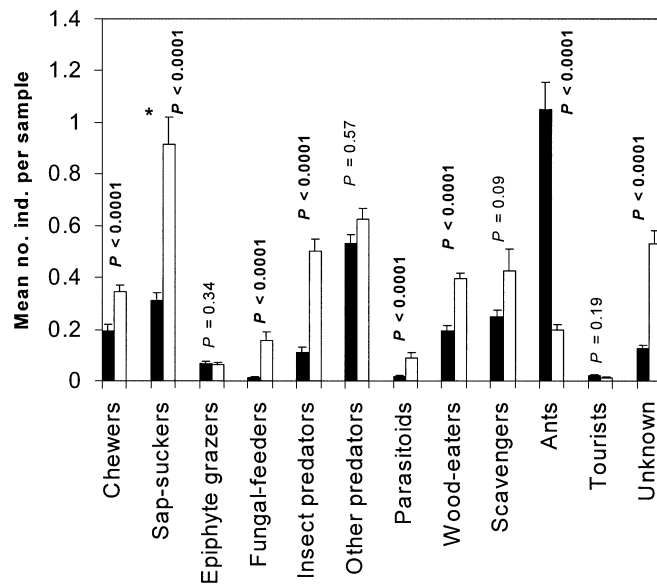


Fig. 1 Distribution of arboreal guilds on saplings (closed black bars) and mature trees (open white bars) of *Pourouma bicolor*. Error bars represent SE and probabilities indicate the result of Mann-Whitney tests. *For the sake of clarity, values were divided by a factor of 2 for sap-suckers. ind. Individuals

spectively; Mann-Whitney $U=357,132$, $P<0.0001$). Leaf-chewing and sap-sucking insects, as well as fungal-feeders, insect predators, parasitoids and wood-eaters, were significantly more abundant on trees than on saplings, whereas ants showed the reverse trend (Fig. 1).

Insect herbivores were about 2.5 times as abundant on the foliage of trees as on that of saplings (average 2.574 ± 0.216 and 1.015 ± 0.066 individuals, respectively; Mann-Whitney $U=299,775.5$, $P<0.0001$). Of the three guilds of herbivores, sap-suckers showed most differences, being 2.9 as abundant in trees as in saplings (Fig. 1). Densities of leaf-chewing insects feeding on *P. bicolor* were also 2.9 times as high on trees as on saplings. Conversely, densities of non-feeding chewers were marginally higher on saplings than on trees (Table 2). Thysanoptera, Achilixiidae, Tingidae, Chrysomelidae and Curculionidae were overall significantly more abundant on trees than on saplings, whereas Apionidae and Lepidoptera showed the reverse trend (Table 2).

A total of 248 species were sorted from the herbivore material collected on *P. bicolor*. Twenty-seven species of weevils had to be assigned to the unknown category and were not considered in the analyses. Of the 25 leaf-chewing species recorded feeding on *P. bicolor* (Table 3), all but one fed on young foliage. For an equal sample size of leaf area, the species richness of herbivores was about 1.5 times as high on trees as on saplings (species observed, Table 3). However, for a rarefied set of 400 individuals, herbivore collections were richer on saplings than on mature trees, and the Chao1 index sug-

Table 2 Mean number of individuals (SE in parentheses) and total number of species for higher taxa of insect herbivores collected on saplings and mature trees. Mann-Whitney U -tests for difference in abundance between host stages and Fisher's exact test for a similar proportion of herbivore species being collected from both host stages (probabilities in *italics* are significant after Bonferroni's

correction). Mann-Whitney U further test difference in abundance between host stages at the species level. *Total* Number of species common enough to be analysed, *Sign.* number of species significant after Bonferroni's correction, *S* more abundant on saplings, *T* more abundant on trees

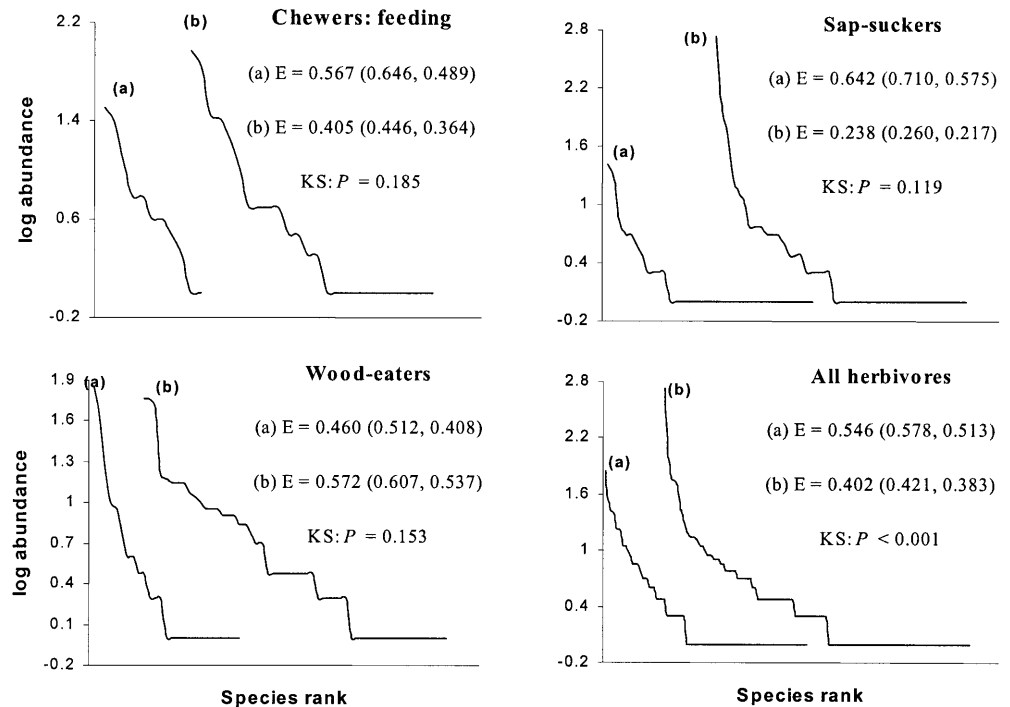
Taxa/group tests	Mean no. of individuals		Mann-Whitney	No. of species		Fisher	Species level	
	Saplings	Trees	<i>P</i>	Saplings	Trees	<i>P</i>	Total	Sign.
Chewers								
All leaf-chewers: feeding	0.095 (0.026)	0.275 (0.024)	<i>P</i> <0.0001	6	21	0.060	5	1S, 3T
All leaf-chewers: not feeding	0.097 (0.010)	0.066 (0.009)	0.006	29	29	0.091	1	0
Chrysomelidae	0.046 (0.007)	0.218 (0.022)	<i>P</i> <0.0001	17	19	0.361	2	2T
Apionidae	0.045 (0.007)	0.016 (0.004)	<i>P</i> <0.0001	6	4	0.205	1	0
Curculionidae ^a	0.016 (0.004)	0.015 (0.004)	0.914	6	7	0.773	0	—
Lepidoptera	0.076 (0.026)	0.065 (0.009)	0.002	4	8	0.767	3	1S, 1T
Sap-suckers								
Thysanoptera	0.002 (0.001)	0.463 (0.069)	<i>P</i> <0.0001	1	1	1.000	1	0
Aleyrodidae	0.223 (0.035)	0.318 (0.195)	0.526	0	2	0.518	1	1T
Derbidae	0.022 (0.005)	0.007 (0.003)	0.013	11	2	0.001	0	—
Cicadellidae	0.091 (0.015)	0.082 (0.009)	0.042	8	11	1.000	1	1S
Membracidae	0.059 (0.026)	0.062 (0.019)	0.279	4	11	0.415	1	0
Wood-eaters								
Curculionidae ^b	0.180 (0.19)	0.388 (0.022)	<i>P</i> <0.0001	22	51	0.045	9	2S, 4T

^a Leaf-chewers only

^b Wood-eaters only

Table 3 Estimators of species richness for different herbivore guilds on saplings and trees of *P. bicolor*. Ind. Number of individuals considered for the rarefaction with Coleman's curve

Guild	No. of species observed			Chao1 $\pm$ SD		Coleman $\pm$ SD		Ind.
	Total	Saplings	Trees	Saplings	Trees	Saplings	Trees	
Chewers: feeding	25	6	21	6.0 $\pm$ 0	80.5 $\pm$ 71.1	6.0 $\pm$ 0.1	10.2 $\pm$ 1.8	70
Chewers: not feeding	49	29	29	274.0 $\pm$ 263.5	76.1 $\pm$ 31.4	24.1 $\pm$ 2.3	29.1 $\pm$ 1.3	60
All chewers	74	34	47	124.3 $\pm$ 76.7	119.9 $\pm$ 43.9	31.9 $\pm$ 1.4	37.4 $\pm$ 2.6	150
Sap-suckers	76	37	43	121.5 $\pm$ 54.5	102.6 $\pm$ 35.7	34.0 $\pm$ 1.6	11.7 $\pm$ 2.3	90
Wood-eaters	71	26	55	59.7 $\pm$ 26.3	82.0 $\pm$ 17.6	24.1 $\pm$ 1.5	38.3 $\pm$ 2.8	150
All herbivores	221	97	145	291.4 $\pm$ 83.0	295 $\pm$ 53.1	90.7 $\pm$ 2.5	76.3 $\pm$ 5.0	400

Fig. 2 Species-abundance distribution of herbivore guilds on saplings (a) and trees (b). The index of evenness (*E*) and its 95% confidence limits are indicated for each curve, with the results of the Kolmogorov-Smirnov two sample tests (*KS*)

gested that the overall species richness was similar on both host stages (Table 3). The pattern was similar for sap-sucking insects, with the Chao1 estimator even slightly higher for collections obtained from saplings than for those from trees. The species richness and the Coleman estimator for chewers overall were higher on trees than on saplings, but these differences were small. However, the rarefied estimates, the observed number of species and the overall number of species of chewers known to feed on *P. bicolor* were 1.7, 3.5 and 13.4 times higher on trees than on saplings, respectively. In contrast, estimates of species richness of chewers not feeding on *P. bicolor* were not very different between collections obtained from saplings and trees, with the exception of the overall species richness being higher for the former than the latter. The three types of richness estimators suggested that wood-eaters were more speciose on trees than on saplings, but the magnitude of difference was not as high as for proven chewers (Table 3).

The structure of herbivore communities foraging either on saplings or on trees, as estimated by the species-

distribution and evenness of distribution within the community (Fig. 2), were significantly different overall (Kolmogorov-Smirnov two sample test, Fig. 2). However, the rank abundance of communities of proven chewers, sap-suckers or wood-eaters were not significantly different on saplings and trees. The distribution of individuals within sapling communities was usually more even than within tree communities (Bulla's *E*, Fig. 2). The distribution of insect species within herbivore families was usually uniform on either saplings or trees (Table 2). However, of 21 herbivore species that were amenable to statistical analysis (Table 2; two species of Achilixiidae and Tingidae are not accounted for, and both were significantly more abundant on trees), seven species showed no significant preference for either saplings or trees and 14 species showed significant preferences, after considering Bonferroni's correction. The latter group included ten species which preferred trees (including seven species not collected at all on saplings) and four species which preferred saplings (including three species not collected at all on trees).

The average area of young foliage surveyed within samples was significantly higher on trees than on saplings (202 ± 11 cm² and 72 ± 10 cm², respectively; $t = -4.34$, $P < 0.0001$). The coefficient of variation of leaf production during surveys 1–25 was also significantly lower for trees than for saplings ($t = 2.878$, $P < 0.01$). The total inertia of the DCA was 4.851, with Fig. 3a representing 29% of the total variance in the system. The analysis grouped

the trees together, along with a suite of herbivore species which preferred this stage. The CCA grouped the herbivore species in a similar way than to the DCA for the first four axes ($r = 0.99$, 0.98 , 0.86 and 0.85 , respectively; $P < 0.05$ in all cases). The total sum of eigenvalues in the CCA was 2.482, indicating that the eight constraining variables explained about 51% of the total variance in the system. The first canonical axis accounted for 32% of the variance explained by the CCA, the second 20%, the third 14% and the fourth 11%. Fig. 3b explained 52% of variance in the constrained system and 26% of variance in the real matrix of observations. The best explanatory variables for the formation of axes 1 and 2 were host stage and the average area of young foliage, respectively (Table 4, correlation coefficients, $P < 0.05$). The formation of the other axes was more difficult to infer from the explanatory variables. The relation between the species and the environmental variables was highly significant (Monte Carlo test, 199 permutations, $F = 2.36$, $P < 0.001$).

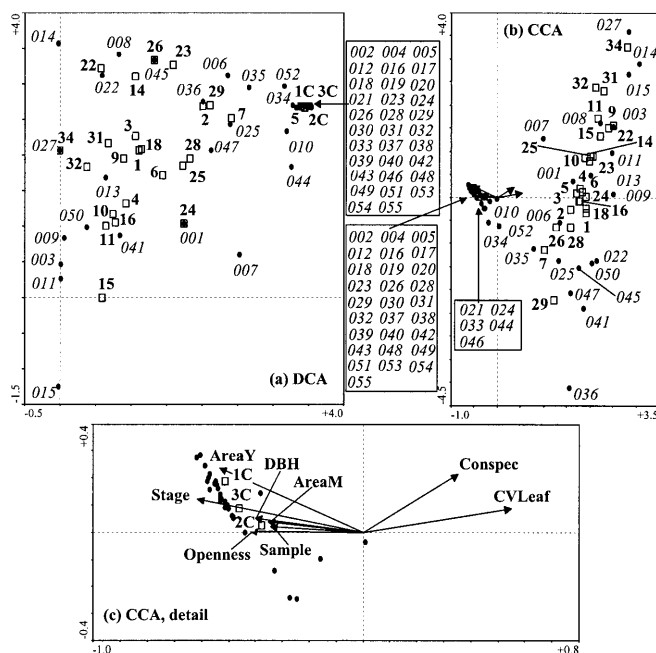


Fig. 3a–c Ordinations of 55 species of herbivores (closed circles with digits in italics) across the 28 study plants (open squares with numbers in bold, coded as in Table 1). Plots of the species and plants into axes 1 and 2 of the **a** detrended correspondence analysis (DCA) and **b** canonical correspondence analysis (CCA). **c** Detail of the CCA plot, near the origin. Codes for herbivore species identified at least to generic level. 004 *Coelomera* sp.; 005 *Antitypona* sp.; 006 *Allocolapsis* sp.; 007 *Monomacra* sp.; 010 *Exostalmus* sp.; 011 *Bagous* sp.; 012 *Heilipus draco* F.; 013 *Gonioterma seppiana* Stoll; 017 *Bebaiotes* sp.; 022 *Anormenis* sp.; 023 *Epipolops mucronatus* Distant; 025 *Bolbonota* sp.; 029 *Macrotingis zeteki* Drake; 033, 034, 041, 042, 046, 050, 052 *Eulechriops* sp.; 031, 032, 035–040, 043, 044, 045, 047, 048, 049, 051, 053, 054, 055 *Lechriops* sp.

Discussion

Pseudo-replication and host representativeness

Good access to and sampling from the upper canopy is troublesome (e.g. Basset et al. 1992). The present study, one of the first reporting on faunal differences between host stages in a tropical rainforest, investigated only three mature trees and 25 conspecific saplings. Although pseudo-replication may have affected the data, the true degree of freedom of Mann-Whitney tests may vary between 1 (only host stages different) and 1,998 (all samples different). Most likely, the main effects of pseudo-replication in the present study may have been to lower the magnitude of differences observed between saplings and trees. Had 25 mature trees been investigated over the 6-ha plot, they would have probably supported more herbivore species than reported here (as suggested by Chao1 estimates). Furthermore, samples obtained from saplings were on average 7% larger than those obtained from trees, yet yielded fewer arthropods. Saplings were also devoid of reproductive structures and of the fauna exploiting these resources. Thus, differ-

Table 4 Canonical coefficients and intraset correlations for environmental variables included in the canonical correspondence analysis; for other abbreviations, see Table 1

Variable	Canonical coefficients				Correlation coefficients			
	Axis 1	Axis 2	Axis 3	Axis 4	Axis 1	Axis 2	Axis 3	Axis 4
Host stage	-1.269	0.207	3.254	1.018	-0.961	0.241	-0.140	-0.100
DBH	0.978	-2.290	-7.136	-3.494	-0.625	0.102	-0.035	-0.028
Openness	-1.189	-1.844	-1.018	1.374	-0.651	0.003	-0.094	0.043
Total leaf area mature	0.268	7.798	14.553	4.133	-0.553	0.077	-0.036	-0.021
Average leaf area young	0.407	0.833	-1.970	-0.604	-0.831	0.458	-0.200	-0.139
CV leaf production	-0.023	-0.010	0.347	-0.288	0.855	0.171	0.092	-0.189
No. conspecifics	0.016	0.267	0.019	0.551	0.548	0.420	-0.103	0.613
No. samples	-0.002	-4.522	-7.634	-2.635	-0.537	0.044	-0.050	-0.032

ences in densities and species richness between saplings and trees reported in this study should be considered as minimum values.

It may also be prudent to examine whether *P. bicolor* is representative of other tree species. Saplings of this pioneer species tend to grow in gaps, where the microclimate may be more similar to upper canopy conditions than in the shaded understorey. Thus, faunal similarity between saplings and mature trees could be higher for *P. bicolor* than for shade-tolerant species. Further, herbivore species richness on this host appeared to be rather low, as compared with other tropical hosts (e.g. Basset 1996; Basset and Novotny 1999), and faunal differences may well be more pronounced on tree species supporting a diverse fauna of herbivores.

Salient differences in the arthropod fauna foraging on saplings and trees

Arthropods were about 1.6 times as abundant on the foliage of trees as on saplings, and many arthropod guilds or taxa were more abundant or speciose on trees than on saplings. Notable exceptions were taxa well-represented in the soil/litter habitat, such as the scavenging fauna and other predators (mostly spiders). Ants were also more abundant on saplings than on trees. Although many studies reported a high abundance of ants in the canopy of rainforests (e.g. Basset et al. 1992), this often depends on a few ant species feeding on plant and homopteran exudates in the canopy (Davidson 1997). On *P. bicolor* trees, ants were rarely observed tending homopterans.

For a similar leaf area sampled, insect herbivores were 2.5 times as abundant and 1.5 times as species-rich on the foliage of trees as on saplings. This included many wood-eating Zygopinae of the genera *Lechriops* and *Eulechriops*, widely known to feed on the pith of leaf petioles of Cecropiaceae (Jordal and Kirkendall 1998). Overall, sap-sucking insects were more abundant on trees than on saplings, but this was mainly due to the occurrence of the achilixii *Bebaiotes* sp., whose life cycle remains unknown. The most extreme differences between the fauna of saplings and trees were demonstrated by the leaf-chewing species with a proven ability to feed on the foliage of *P. bicolor*. This guild was 2.9 times as abundant and 3.5 times as species-rich on trees as on saplings. Chao1 estimates even suggested that differences in species richness could be much higher. In contrast, on *Quercus* spp. in the USA, more leaf-chewing species fed on sapling than on conspecific trees, and none were restricted to the canopy (Le Corff and Marquis 1999).

However, few differences between saplings and trees existed when non-feeding individuals or all species of leaf-chewing insects were considered. Thus, it is crucial to ascertain the ability of insects to feed on the foliage of study plants and to remove transient species (Basset 1999). Sap-sucking data, therefore, must be considered with caution.

Availability of food resource in the upper canopy

For a similar sampling effort, about 3 times more young foliage was surveyed on trees than on saplings. This indicates that the availability of food resources was higher, and perhaps also more predictable (cf. lower coefficient of variation of leaf production), in the upper canopy than in the understorey. The ordinations confirmed that variables which best accounted for the variance in the distribution of herbivore species were host stage and young foliage, which, together, explained 52% of the variance explained and 26% of the variance in the real matrix of observations. The dependence of proven chewers on young foliage was not surprising since 96% of species feed only on young foliage of *P. bicolor*. Their rank-abundance plots and evenness on trees suggest that their communities there may be dominated by a few species well-adapted to upper canopy conditions, in contrast with communities on saplings, which are less species-rich and more even.

In addition to the availability of young foliage, other factors may cause the foliage of saplings and trees of *P. bicolor* to be very different media for insect herbivores. These may be related to: (1) microclimate; (2) leaf palatability; and (3) enemy-free space. Microclimatic effects must be consequent and may represent a behavioural barrier for many insects dispersing either in the sunny upper canopy or shady understorey (e.g. Moore et al. 1988). The main factors affecting leaf palatability may include leaf toughness and chemistry, since leaf pubescence appears superficially similar on both host stages. Tree leaves are tougher and, when damaged, exude more latex than sapling leaves (Y. Basset, personal observation). If overall leaf palatability is higher on trees than on saplings, then the foliage of saplings must be extremely well-defended, as has been found in tropical trees (e.g. Langenheim and Stubblebine 1983). Finally, the abundance of insect predators and parasitoids was higher on trees than on saplings, ants showing the reverse trend and other predators (mostly spiders) being similarly abundant on both host stages. However, it is difficult to comment on the significance of enemy-free space without examining prey-predator relationships case by case.

Conclusions

Different herbivore communities exploit different host stages, generating a vertical stratification of organisms on *P. bicolor*. Several studies reported convincing faunal differences between the understorey and upper canopy of wet tropical rainforests (e.g. Rodgers and Kitching 1998; Walter et al. 1998; Basset et al. 1999). However, the present work demonstrated such stratification on a discrete resource (*P. bicolor*), suggesting a mechanism by which biodiversity may be greatly enhanced in tropical closed rainforests. It is probable that the magnitude of faunal differences between the understorey and upper canopy may depend on both forest type and plant species. The clear-cut differences reported here for a pioneer species such as *P. bicolor* are surpris-

ing and suggest that shade-tolerant tree species may induce an even more extreme faunal stratification. One essential difference between temperate and tropical wet forests may well prove to be the lack of pronounced vertical gradients in the former, due to the less drastic vertical changes in microclimate and biotic factors there. Vertical gradients of species richness within wet tropical rainforests may be akin to gradients of latitudinal richness, when resulting from the control of solar energy over organic diversity in conditions of non-limited water resources (Turner et al. 1987).

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References

- Barone JA (2000) Comparison of herbivores and herbivory in the canopy and understory for two tropical tree species. *Biotropica* 32:307–317
- Basset Y (1996) Local communities of arboreal herbivores in Papua New Guinea: predictors of insect variables. *Ecology* 77:1906–1919
- Basset Y (1999) Diversity and abundance of insect herbivores collected on *Castanopsis acuminatissima* (Fagaceae) in New Guinea: relationships with leaf production and surrounding vegetation. *Eur J Entomol* 96:381–391.
- Basset Y, Novotny V (1999) Species diversity of insects herbivores on *Ficus* spp. in Papua New Guinea. *Biol J Linn Soc* 67:477–499
- Basset Y, Aberlenc H-P, Delvare G (1992) Abundance and stratification of foliage arthropods in a lowland rain forest of Cameroon. *Ecol Entomol* 17:310–318
- Basset Y, Charles EC, Novotny V (1999) Insect herbivores on parent trees and conspecific seedlings in a Guyana rain forest. *Selbyana* 20:146–158
- Blanc P (1990) Bioclimatologie comparée de la canopée et du sous-bois. In: Hallé F, Blanc P (eds) *Biologie d'une canopée de forêt équatoriale. Rapport de Mission Radeau des Cimes Octobre–Novembre 1989, Petit Saut – Guyane Française*. Montpellier II, CNRS-Paris VI, Montpellier, Paris, pp 42–43
- Borcard D, Legendre P, Drapeau P (1992) Partialling out the spatial component of ecological variation. *Ecology* 73:1045–1055
- Bulla L (1994) An index of evenness and its associated diversity measure. *Oikos* 70:167–171
- Colwell RK (1997a) Biota: the biodiversity database manager. Sinauer, Sunderland
- Colwell RK (1997b) EstimateS: statistical estimation of species richness and shared species from samples. Version 5. User's guide and application published at: <http://viceroy.eeb.uconn.edu/estimates>
- Colwell RK, Coddington JA (1994) Estimating terrestrial biodiversity through extrapolation. *Phil Trans R Soc Lond Ser B* 345:101–118
- Condit R (1998) Ecological implications of changes in drought patterns: shifts in forest composition in Panama. *Climatic Change* 39:413–427
- Davidson DW (1997) The role of resource imbalances in the evolutionary ecology of tropical arboreal ants. *Biol J Linn Soc* 61:153–181
- Fowler SV (1985) Difference in insect species richness and faunal composition of birch seedlings, saplings and trees: the importance of plant architecture. *Ecol Entomol* 10:159–169
- Frankie GW, Baker HO, Opler PA (1974) Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. *J Ecol* 62:881–913
- Janzen DH (1970) Herbivores and the number of tree species in tropical forests. *Am Nat* 104:501–528
- Jordal BH, Kirkendall LR (1998) Ecological relationships of a guild of tropical beetles breeding in *Cecropia* petioles in Costa Rica. *J Trop Ecol* 14:153–176
- Kobe RK (1999) Light gradient partitioning among tropical tree species through differential seedling mortality and growth. *Ecology* 80:187–201
- Langenheim JH, Stubblebine WH (1983) Variation in leaf resin between parent tree and progeny in *Hymenaea*: implications for herbivory in the humid tropics. *Biochem Syst Ecol* 11:97–106
- Lawton JH (1983) Plant architecture and the diversity of phytophagous insects. *Annu Rev Entomol* 28:23–29
- Le Corff J, Marquis RJ (1999) Differences between understorey and canopy in herbivore community composition and leaf quality for two oak species in Missouri. *Ecol Entomol* 24:46–58
- Leigh EG Jr (1994) Do insect pests promote mutualism among tropical trees? *Ecology* 82:677–680
- Macedo CA, Langenheim JH (1989) Microlepidopteran herbivory in relation to leaf sesquiterpenes in *Copaifera langsdorffii* adult trees and their seedling progeny in a Brazilian woodland. *Biochem Syst Ecol* 17:217–224
- Magurran AE (1988) Ecological diversity and its measurement. Croom Helm, London
- Moore LV, Myers JH, Eng R (1988) Western tent caterpillars prefer the sunny side of the tree, but why? *Oikos* 51:321–326
- Moran CV, Southwood TRE (1982) The guild composition of arthropod communities in trees. *J Anim Ecol* 51:289–306
- Parker GG (1995) Structure and microclimate of forest canopies. In: Lowman MD, Nadkarni NM (eds) *Forest canopies*. Academic Press, San Diego, Calif., pp 431–455
- Price PW (1992) The resource-based organization of communities. *Biotropica* 24:273–282
- Rodgers DJ, Kiching RL (1998) Vertical stratification of rainforest collembolan (Collembola: Insecta) assemblages: description of ecological patterns and hypotheses concerning their generation. *Ecography* 21:392–400
- Root RB (1973) Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). *Ecol Monogr* 43:95–124
- Roubik DW (1993) Tropical pollinators in the canopy and understorey: field data and theory for stratum “preferences”. *J Insect Behav* 6:659–673
- Schowalter TD, Ganio LM (1998) Vertical and seasonal variation in canopy arthropod communities in an old-growth conifer forest in southwestern Washington, USA. *Bull Entomol Res* 88:633–640
- Strong DRJ (1977) Rolled-leaf hispine beetles (Chrysomelidae) and their Zingiberales host plants in middle America. *Biotropica* 9:156–169
- Sutton SL (1983) The spatial distribution of flying insects in tropical rain forests. In: Sutton SL, Whitmore TC, Chadwick AC (eds) *Tropical rain forest: ecology and management*. Blackwell, Oxford, pp 77–92
- Ter Braak CJF, Smilauer P (1998) CANOCO Reference manual and user's guide to Canoco for Windows: software for canonical community ordination (version 4). Microcomputer Power, Ithaca, N.Y.
- Tokeshi M (1993) Species abundance patterns and community structure. *Adv Ecol Res* 24:111–186
- Turner RG, Gatehouse CM, Corey CA (1987) Does solar energy control organic diversity? Butterflies, moths and the British climate. *Oikos* 48:195–205
- Walter DE, Seeman O, Rodgers D, Kitching RL (1998) Mites in the mist: how unique is a rainforest canopy-knockdown fauna? *Aust J Ecol* 23:501–508
- Woodson RE, Schery RW (1960) Flora of Panama, part iv, fascicle 2: Moraceae. *Ann Miss Bot Gard* 47:114–178
- Wright SJ, Colley M (1996) Tropical forest canopy programme. UNEP/STRI, Nairobi