Selbyana 20(1): 146–158. 1999.

INSECT HERBIVORES ON PARENT TREES AND CONSPECIFIC SEEDLINGS IN A GUYANA RAIN FOREST

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ABSTRACT. More than 14,500 insect herbivores were collected in a rain forest in Guyana from 10,000 seedlings belonging to five plant species, their parent trees, and the forest understory. In October 1997, half (125) of the parent trees were felled to mimic selective logging. In this paper, we compare the insect fauna collected on the seedlings with that on the foliage of felled trees and discuss the findings with regard to the collections made in the understory. For a similarly sized sample, the foliage of felled trees yielded more than twice the number of insect species and 1.5 times as many individuals as did seedlings. More xylem-feeding Cicadellinae were collected from the seedlings, whereas more Acanaloniidae, Issidae, Flatidae, Tropiduchidae, and Lepidoptera were collected from the foliage of felled trees. Comparisons were complicated by the influx of understory species into the foliage of trees after felling. The dissimilarity of the data between seedlings and felled trees and the rather restricted occurrence of common insect species on the foliage of either seedlings or felled trees suggest, however, that few insect species forage both on seedlings and in the crowns of parent trees. Most species instead exploit the resources available either in the understory or in the canopy.

Key words: canopy, insects, herbivores, Guyana, seedlings, understory

INTRODUCTION

Local insect and plant richness in tropical rain forests may be constrained by several historical and ecological factors. For leaf-feeding insects, local ecological factors accounting for resource availability and predictability appear to be particularly important (e.g., Strong 1977a, 1977b, Gilbert & Smiley 1978, Marquis 1991, Lewinsohn 1991, Basset 1996). Often, insect herbivory in rain forests is concentrated on young leaves, since those frequently are more palatable and tender than mature leaves (e.g., Coley 1983). The production and palatability of young leaves in tropical trees, as well as the abundance and foraging patterns of insect herbivores, may be affected drastically by the light regime (e.g., Aide & Londoño 1989, Basset 1992). The resources, as well as the diversity of habitats, available to insect herbivores, therefore, may be much higher in the canopy than in the less well illuminated lower strata of the forest. Insect abundance and diversity hence may differ considerably between different layers of the forest.

Many studies in rain forests report a higher abundance, activity, or diversity of insect herbivores in the canopy than in the understory (e.g., Wolda 1979, Sutton 1983, Basset et al. 1992). These studies, however, compared whole forest strata rather than specific resources available to insect herbivores in these strata. With one exception (Basset et al. 1992), samples were not standardized for the much higher plant biomass in the canopy, as compared with the understory. Comparison of the insect communities feeding on conspecific mature trees, saplings, and seedlings may represent a more rigorous method by which differences in insect abun-

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dance and diversity between the canopy and the understory can be tested. The resource provided by the different host forms may explain a substantial part of the variance in insect abundance and/or diversity between the canopy and understory.

Several studies have examined the insect fauna feeding on seedlings of tropical trees and/or the leaf damage sustained by such seedlings (e.g., Becker 1983, Clark & Clark 1985, Langeheim & Stubblebine 1983, Cruz & Dirzo 1987). Few, however, have compared specifically the insect fauna feeding on conspecific mature trees and seedlings, with the notable exception of Fowler (1985) who studied birch insects in Great Britain (see Godfray 1985). Fowler concluded that few faunal differences existed between mature trees and seedlings, but his samples were obtained only from sun leaves. Furthermore, his sampling effort was partially controlled; therefore, the interpretation of his results is not straightforward.

In tropical rain forests, strong differences are expected among insect communities feeding on conspecific mature trees, saplings, and seedlings; the reason being that the amount and quality of resource, as well as the number of habitats provided by these host forms, may be drastically different, unlike in temperate forests. For example, most mature rain forest trees are taller than their conspecific seedlings by at least a factor of 100, in comparison to a factor of 30 in the birch studies by Fowler. The potential for insects being restricted in certain habitats in highly heterogeneous tropical forests is also much greater than in more homogeneous temperate forests. Further, illumination patterns may have a greater influence on insects in tropical forests than in temperate forests, since differences in illumination between canopy and understory are more marked in tropical forests than in temperate ones (see Blanc 1990). Since the resource base on which a community is founded may influence many aspects of trophic structure, including the number of species in food-webs (Price 1992), rain forest seedlings may be expected to support a lower insect species richness than mature trees. Other insect variables, however, may differ between conspecific mature trees and seedlings, such as the density of herbivores or the proportion of specialist or generalist species; many insect species may be canopy specialists in addition to being restricted to certain host plants (Erwin 1983). Some of these differences could have implications for tree regeneration in tropical forests, both from an ecological and evolutionary perspective.

Much of the attention, however, has focused on the actual damage and mortality sustained by rain forest seedlings rather than on the insect species responsible for damage (e.g., Becker 1983, Clark & Clark 1985, Cruz & Dirzo 1987, Aide 1991). The occurrence of the insects responsible for leaf damage rarely has been detailed (e.g., Folgarait et al. 1995, Gombauld 1996; see New 1983 and Heatwole et al. 1997 for acacia seedlings and eucalypt saplings in Australia). Seminal works such as those by Fowler (1985) and Godfray (1985), comparing the communities of insect herbivores feeding on birch seedlings and parent trees in the UK, to date have not been followed in natural habitats in the tropics. These data, which are sadly missing, could help botanists comprehend patterns of attack on seedlings, perhaps as a result of insect dispersal or contagion from parent trees.

Many studies addressing herbivory on seedlings have focused on testing whether the Janzen-Connell model could be substantiated (e.g., Wilson & Janzen 1972, Augspurger 1984, Condit et al. 1992). The model states that patterns of herbivore attack below the parent tree are density-dependent and decrease with increasing distance to the parent tree (Janzen 1970, Connell 1971). One of the implicit assumptions of the model is that most insect herbivores that feed on seedlings are specialists that also may feed on parent trees (Leigh 1994). Rarely has this assumption been tested adequately. Testing this and related hypotheses appears crucial for a better understanding of the evolution of mechanisms maintaining local diversity of both plant and insect taxa in tropical rain forests.

Within the context of a larger study investigating the effects of selective logging on insects foraging on seedlings in a rain forest in Guyana, parent trees were felled and their foliage examined for insect herbivores. The study examined faunal differences between the foliage of felled trees and their conspecific seedlings. Although this procedure is far from being ideal, the study is motivated by the almost complete lack of data comparing insect fauna feeding on parent trees and their conspecific seedlings in tropical rain forests.

MATERIALS AND METHODS

Study Sites and Study Plants

Insect sampling was performed in a plot of 0.92 km^2 of unlogged forest (Block 17) in the Camoudi compartment of the logging concession of Demerara Timbers Limited, some 40 km south of Mabura Hill, central Guyana (5°13′N, 58°48′W, ca. 30 m altitude). The main forest types in Block 17 include well and poorly drained mixed forests (ter Steege et al. 1996).

Annual rainfall at Mabura Hill is high and variable, 2500–3400 mm, while annual air temperature is about 25.9°C. A long wet season usually occurs between May and August and a short one, between December and February (ter Steege et al. 1996).

This study focused on seedlings and on foliage of felled trees of the following species, which are either valuable timber species in Guyana or relatively common in Block 17: *Chlorocardium rodiei* (Scomb.) (Lauraceae, Greenheart); *Mora gonggrijpii* (Kleinh.) Sandw. (Caesalpiniaceae, Morabukea); *Eperua rubiginosa* Miq. (Caesalpiniaceae, Water Wallaba); *Pentaclethra macroloba* (Willd.) Kuntze (Mimosaceae, Trysil); and *Catostemma fragrans* Benth. (Bombacaceae, Sand Baromalli). Hereafter, they are designated by their generic names. All species can be classified as shade-tolerant. A collecting station was defined as a fixed number of tagged seedlings (40 for *Chlorocardium* and *Catostemma,* 50 for *Mora* and *Eperua,* and 15 for *Pentaclethra*) growing below the parent tree or in its vicinity. Fifty such collecting stations were chosen for each species in Block 17 (total 250 stations and 9750 seedlings). As far as possible, stations were interspersed in the study site and experienced different light regimes. Non-tagged seedlings growing below the parent tree replaced tagged seedlings that died during the course of the study. On average, seedling leaf area increased by 4.7% at the end of the sampling program. Other characteristics of the study site, stations, and plants are detailed elsewhere (Basset 1999).

Insect Collecting and Processing

This paper compares four different datasets, all collected in Block 17, mostly during 1997: insects foraging on seedlings, insects on foliage of felled parent trees, insects foraging on saplings of *Eperua,* and insects collected in the understory. The sampling protocols targeted free-living insect herbivores collected during daytime, by hand or with small aspirators. They included leaf-chewing (e.g., Chrysomelidae, some Curculionidae, juvenile Lepidoptera, some Orthoptera) and sap-sucking insects (many Homoptera and Heteroptera). Although the protocol for seedling insects is detailed below, other datasets were obtained with similar and comparable methods.

Insects foraging on seedlings

Most of the collecting was performed by field assistants trained for this purpose. From October 1996 to September 1997, a total of 11 monthly insect surveys were organized. During each survey, all tagged seedlings of the 250 collecting stations were inspected once, during daytime. As far as possible, insects that flew away were recorded to the insect family. On average, one assistant spent at least 30 minutes at each collecting station, carefully inspecting each tagged seedling. During each survey, groups of closely situated stations were assigned to four or five assistants in a random fashion to reduce the collector's effect. Juveniles of leaf-chewing insects (all caterpillars) were collected and reared with young foliage from seedlings grown for this purpose. Juveniles of sap-sucking insects were not collected but recorded to the nearest insect family.

At each station and for each seedling, the assistants recorded the number of mature and young leaves present, the latter lacking the typical texture and pigmentation of the fully expanded leaves. A rough estimate of the leaf area sampled at each station during each survey was computed by multiplying the number of young and mature leaves recorded by the average specific leaf area (detailed in Basset 1999). The average total leaf area monitored at each station varied from about 0.5 m^2 (*Chlorocardium*) to 3.0 m^2 (*Mora*). Given the extremely low insect densities recorded, these differences in sample size were neglected, and unadjusted densities were considered in the analyses (Basset 1999).

Leaf-chewing insects were kept in plastic vials with young leaves of the host-plant species on which they were collected. The vials were kept 3–4 days in Block 17, and records of leaf damage and frass were subsequently checked. Insect species responsible for obvious damage later were assigned to the "feeding" category, and others, including dead insects, to the "non-feeding" category. Only the former group was later assigned to morphospecies. These simple tests permitted the removal of transients, as well as species infrequently feeding on the seedlings, from the analyses. Using this information, as well as distributional records, we classified both leaf-chewing and sap-sucking insects into "specialists" and "generalists" categories (Basset 1999).

From this rather large dataset, we considered a) all insects collected during surveys 1–11; b) insects collected during September 1997 (Survey 11) just before the felling of the parent trees; c) insects collected on seedlings of *Eperua* in April 1997 (Survey 7) to compare with insects collected simultaneously on *Eperua* saplings; and d) insects collected on seedlings of *Eperua* in September 1997 (Survey 11) to compare with insects collected on felled trees in October 1997.

Insects on foliage of felled parent trees

During October 1997, half of the parent trees at the stations were felled ($N = 125$). This felling mimicked a situation of selective logging, where only particular areas in the forest are cut and damaged. As soon as the trees were felled, their foliage was inspected for insect herbivores. Two types of sampling, quantitative and qualitative, were performed for each felled tree. The quantitative sampling attempted to examine a leaf area for insects within the felled foliage similar to what was inspected during a monthly survey of seedlings. Inspections were made on 200 leaves of felled foliage of *Chlorocardium, Eperua,* and *Catostemma*; on 280 leaves of *Mora;* and on 60 leaves of *Pentaclethra* to equal approximately the leaf area of seedlings inspected at each sampling station. Since only half of the stations were felled, we twice inspected the above numbers of leaves on the foliage of each felled parent tree (Subsamples 1 and 2). Thus the total leaf area inspected from the felled foliage was similar to that inspected during the whole of a seedling survey. The assistants proceeded by batches of 20 leaves, recording the presence of young leaves. Their time inspecting the foliage of one felled tree was similar to that spent during the sampling of the tagged seedling of a station. Further, at each station, three leaves randomly were collected and later measured with a leaf area meter to derive a crude estimate of the leaf area inspected.

When the qualitative sampling was finished at one station, the assistants performed additional qualitative sampling by striking the foliage over beating trays. At each station the foliage was hit hard from above with three strokes, and this operation was repeated 10 times (= 10 replicates). As during the seedling surveys, the assistants recorded any insect flying away during either the quantitative or qualitative sampling. Leaf-chewing insects also were tested for positive feeding, following the same protocol used for seedling insects.

Insects on *Eperua* saplings

Insect herbivores were collected alive by hand from *Eperua* saplings in Block 17. Some 275 saplings of 2.5–5 m high were searched thoroughly for insects in April 1997. The area of young and mature foliage was approximated by counting the number of young and mature leaves on each sapling. A sample consisted of three saplings surveyed next to each other. Leaf-chewing insects again were tested for feeding.

Understory insects

During a study of the effect of natural gap size on insect herbivores (E. Charles et al. in prep.), insect herbivores were collected from 15 gaps in Block 17, during a total period of 8 months, from January to August 1997. These gaps were assigned to three categories of size: small (50–150 m^2), medium (200–300 m^2), and large (350–895 m^2). Insect sampling was restricted to daytime and to vegetation lower than 2 m. Each gap was surveyed twice monthly. A survey in a particular gap consisted of randomly selecting four quadrats of 1 m^2 each, which were surveyed for 4 consecutive days (10 minutes spent collecting at each quadrat daily). Around 213 hours were spent collecting insects in each gap category during the course of the study. In opposition to the other insect datasets, the collections in the understory did not target particular host plants and were not related to a known leaf area. From this dataset, we considered a) all insects collected during Surveys 1–8 and b) insects collected during the last survey in August 1997, for ease of comparison with the seedling and tree data.

Insect processing was similar for the four datasets. Live insects were brought to the insect laboratory in Mabura Hill, killed by storage in a freezer for several hours, mounted on points, dried and identified by a personal accession number. Insects then were sorted by morphospecies (hereafter "species" for sake of simplicity) and given a species code, using reference collections and a computer-aided identification guide that stored digital pictures of the specimens, text fields, and sketches of genitalia (Novotny et al. 1997). Routine checking of genitalia was performed only in doubtful cases on male material. Species were all cross-assigned among the four main datasets. The faunistic composition of the material collected is detailed in Basset (1999) and E. Charles et al. (in prep.).

Statistical Analyses

Since insect seasonality in this system was not pronounced, it appeared valid to compare data collected in August (understory), September (seedlings), and October 1997 (felled trees). Thus we first compared seedling, tree, and understory data by cluster analyses. The unweighted arithmetic average clustering method (UPGMA) with Euclidean distances was used on the following subsets of data: Understory Survey 8 (August 1997, 360 insect individuals assigned to species), Seedlings Survey 11 (September 1997, 460 insects), and Trees Quantitative 1 and 2 (October 1997, 331 and 324 insects, respectively). The species richness of these datasets was compared using rarefaction (Hurlbert 1971), with a common sample size of 300 insect individuals. The rarefied datasets, further

TABLE 1. Raw and adjusted data for insect collections in Block 17 of a rain forest of Guyana. Individuals collected and insect abundance, expressed in number of individuals per sample, include juveniles and insects which flew away during collecting.

Insect survey	Ind. collected	No. species	Leaf area sampled m^2	Insect abundance (SE)	Sample leaf area m^2 (SE)
Seedlings—Surveys 1–11	9056	346	4050	3.32 (0.20)	1.47 (0.02)
Seedlings—Survey 11	532	92	368	2.10 (0.14)	1.47 (0.07)
Felled trees—Quantitative	1086	263	583	4.50 (0.15)	2.33 (0.13)
Subsample 1	553	171	291	4.50 (0.25)	2.33 (0.19)
Subsample 2	533	177	291	4.39 (0.26)	2.33 (0.19)
Adjusted data	791	222	347	3.16 (0.16)	1.39 (0.08)
Felled trees—Qualitative	573	152	Not known	—	—
Understory–Survey 1–8	4157	456	Not known	—	—
Understory—Survey 8	379	147	Not known	—	—
Eperua seedlings—Survey 7	321	41	117	5.80 (1.65)	2.33 (0.08)
Eperua seedlings—Survey 11	162	38	118	3.24 (0.41)	2.36 (0.09)
Eperua saplings	821	61	252	8.35 (2.01)	2.75 (0.14)
Felled *Eperua*—Quantitative	219	85	236	4.61 (0.33)	4.72 (0.11)
Adjusted data	112	48	118	2.24 (0.21)	2.36 (0.06)

Note: SE = standard error.

weighted to obtain species abundances totaling 300 insect individuals, were used in cluster analysis, for comparisons with the cluster obtained from raw data.

Comparison of insect densities among different datasets was not straightforward and needed adjustment to a similar sample size, despite attempts in the field to minimize the problem. Since the area of foliage examined for felled trees was higher than that for seedlings (TABLE 1), we adjusted the data by considering only 20 leaves from felled *Pentaclethra,* 100 from *Eperua,* 120 from *Chlorocardium,* 200 from *Mora,* and 200 from *Catostemma.* In this way, we obtained a sample of similar size to that examined for the seedlings. Insect densities at each station, on seedlings and felled trees, were compared using Wilcoxon signed-rank tests (125 pair-wise comparisons). We compared the occurrence of particular insect families or species within samples obtained from seedlings and felled trees, using Mann-Whitney tests without the assumption of tied ranks. The different insect datasets obtained from seedlings, saplings, and felled trees of *Eperua* also were compared, using adjusted data for the latter.

RESULTS

In all, more than 9000 insect herbivores were collected from seedlings, 1500 from the foliage of felled trees, and 4000 from the understory (TABLE 1). These data are difficult to compare directly as sample sizes varied, both in terms of insect individuals collected and area of foliage inspected. Areas of young foliage examined also varied. Virtually no young foliage was recorded from the felled trees in October 1997, whereas in September 1997, the tagged seedlings produced 5.7 m^2 of young foliage. Some subsets of the data, however, appear rather similar in sample size, such as the insects collected on seedlings during Survey 11, the two quantitative subsamples on the foliage of felled trees, and Survey 8 of understory insects. Thus the analyses focused on these data, along with the adjusted dataset for felled trees.

Differences were found in the higher taxonomic composition of the material obtained from the collections (TABLE 2). The foliage of felled trees yielded comparatively more individuals representing fulgoroid families of sap-sucking insects (Acanaloniidae, Dictyopharidae, Fla-

TABLE 2. Insect families (number of individuals) collected in comparative datasets: seedlings (Survey 11), foliage of felled trees (adjusted data) and understory (Survey 8). Mann-Whitney tests compared 250 samples obtained from seedlings and felled trees.

Taxa	Seedlings	Felled trees	Understory	Mann-Whitney *U*
Sap-sucking insects				
Acanaloniidae	0	13	1	32,875***
Achilidae	16	17	25	31,375 n.s.
Aleyrodidae	1	2	7	31,375 n.s.
Cercopidae	2	0	0	31,500 n.s.
Cicadellidae	137	82	78	34,436*
Cixiidae	129	27	15	37,719***
Kinnaridae	4	2	6	31,500 n.s.
Pseudococcidae	0	1	0	31,375 n.s.
Coreidae	0	2	3	31,500 n.s.
Delphacidae	2	8	1	32,000 n.s.
Derbidae	54	63	36	31,862 n.s.
Dictyopharidae	0	13	2	32,875***
Flatidae	0	28	1	34,375***
Fulgoridae	0	1	0	31,375 n.s.
Issidae	3	48	0	35,637***
Membracidae	10	44	43	34,180**
Nogodinidae	0	8	2	32,250**
Pentatomidae	1	3	2	31,500 n.s.
Plataspididae	4	6	1	31,500 n.s.
Psyllidae	55	12	28	33,715**
Tropiduchidae	0	24	1	34,000***
Leaf-chewing insects				
Apionidae	0	0	4	—
Chrysomelidae	37	38	88	30,910 n.s.
Curculionidae	3	19	20	33,001**
Eumastacidae	0	2	0	31,375 n.s.
Tettigoniidae	0	7	0	32,125**
Lepidoptera	7	22	0	33,125**

Note: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, n.s., not significant.

tidae, Issidae, Nogodinidae, and Tropiduchidae) and more Tettigoniidae and Lepidoptera (caterpillars) than the other datasets. High proportions of Cicadellidae (particularly xylem-feeding Cicadellinae), Cixiidae, and Psyllidae were collected from the seedlings, whereas the understory collection yielded comparatively more Chrysomelidae. More Membracidae and Curculionidae were collected from the foliage of felled trees, but these taxa were also abundant in the understory collection (TABLE 2).

Overall, the most speciose insect datasets were in the understory surveys (TABLE 1). These targeted many potential host plants, whereas other datasets focused on one or five host plants. When rarefaction with a common sample size of 300 individuals was applied to each dataset, the most species-rich collections were obtained from the foliage of felled trees (160 and 168 species for subsamples 1 and 2, respectively; 163 species for the adjusted dataset), followed by understory (132 species), and seedlings (72 species).

The cluster analysis of the sub-datasets, concerning 391 insect species, indicated that the two quantitative subsamples of the foliage of felled trees were most similar, followed by the understory insects (FIGURE 1). Seedling insects joined the cluster only distantly. Considering either raw data (FIGURE 1a) or the rarefied data sets (FIGURE 1b) resulted in a similar clustering of the data. In particular, 89 species were common to the two subsamples of felled foliage (out of 259 possible species combinations, 34%); 41 and 45 species from the foliage of felled trees were common to samples obtained from the seedlings (out of 222 and 225 combinations, 19% and 20%, respectively); 45 and 40 species from the foliage of felled trees were common to the understory (out of 273 and 284 combinations, 17% and 14%, respectively); and 24 species were common to seedling and understory samples (215 combinations, 11%). Although the number of singletons (species collected once) was high in all datasets (58–68% of the total species collected), the clustering of the datasets was unchanged when removing singletons or consid-

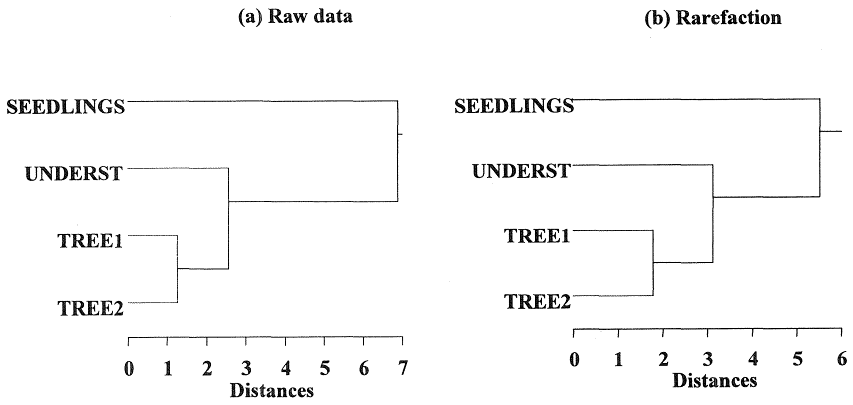

FIGURE 1. Cluster analysis (UPGMA method with Euclidean distances) of the following insect datasets: Survey 11 of seedlings in September 1997 (Seedlings) and quantitative surveys of the foliage of felled trees in October 1997 (Tree1 and Tree2) and of the understory in August 1997 (Underst). Cluster (a) with raw data and cluster (b) with rarefied datasets are set to a common sample size of 300 individuals.

ering only very common species, suggesting that the results were robust.

The most common insect species in each dataset also differed considerably (TABLE 3). An issid dominated the collections made on the foliage of felled trees; and like many other species, it appeared restricted to this dataset. The cixiid *Pintalia* sp. and the cicadellid *Soosiulus fabricii* dominated the collections made on seedlings, whereas the psyllid *Isogonoceraia* sp. dominated the understory collections. *Isogonoceraia* sp., *Pintalia* sp., along with the achilid *Plectoderes collaris,* however, were relatively abundant in all three datasets.

Comparison of Fauna on Seedlings and Foliage of Felled Trees

Specific comparisons were made between seedlings (Survey 11 in September 1997 on 125 stations felled in October 1997) and the foliage of felled trees (Subsamples 1 and 2 adjusted to a similar leaf area of about 1.4 m^2, see TABLE 1). Insect density was found to be significantly higher on felled foliage than on seedlings by a factor 1.5 (TABLE 1; Wilcoxon's test to compare seedlings and Subsample 1, $Z = 4.25$, $P < 0.001$; Wilcoxon's test to compare seedlings and Subsample 2, $Z = 3.53$, $P < 0.001$). When the comparison, however, involved only *Eperua* seedlings and felled *Eperua* trees, insect densities did not differ significantly (comparison with Subsample 1, $Z = -0.507$, $P = 0.612$; comparison with Subsample 2, $Z = 0.122$, $P = 0.902$).

During Survey 11, seedlings that later had their parent tree felled yielded 57 insect species, representing 208 individuals. In comparison, adjusted Subsamples 1 and 2 for the corresponding foliage of felled trees yielded 143 species each, representing 247 and 228 individuals, respectively. Rarefaction of the three datasets to a common sample size of 200 individuals resulted in 130 species for Subsample 1, 123 species for Subsample 2, and 55 species for seedlings.

For species common enough to be analyzed, obvious differences in their occurrence were found in samples obtained from seedlings and from the foliage of felled trees (TABLE 4). Of 25 common species, 15 were significantly more abundant in either type of sample. Three species of Cicadellinae, two of Derbidae, one Cixiidae, and one Psyllidae were significantly more abundant on the seedlings, whereas eight species of Fulgoroidea (various families) were significantly more abundant on the foliage of felled trees.

Since cluster analyses (FIGURE 1) suggested that samples obtained from the foliage of felled trees could be subject to an influx of understory insects, we also compared samples from seedlings and felled trees (Survey 11 for seedlings and adjusted data for felled trees), after removing all insect species also collected in understory samples. After reduction, this rather drastic comparison showed that the foliage of felled trees still supported more insect species (133 species representing 194 individuals) than that of the seedlings (40 species, 58 individuals).

Comparison of Fauna of Seedlings, Saplings, and Felled Trees of *Eperua*

For a similar sample size of about 2.3–2.7 m^2 of *Eperua* foliage, insect densities decreased from the sequence: saplings in April > seedlings in April > seedlings in September > felled trees

TABLE 3. The 10 most common insect species collected on seedlings (Survey 11), on the foliage of felled trees (adjusted data) and in the understory (Survey 8), listed in order of decreasing abundance.

Insect code	Taxa	Identification	No. individuals
A. Seedlings			
1. CIXI006	Cixiidae	*Pintalia* sp.	100
2. CICA004	Cicadellinae	*Soosiulus fabricii* Metcalf	81
3. PSYL003	Psyllidae	*Isogonoceraia* sp.	55
4. CICA010	Cicadellinae	?*Oragua* sp.	15
5. CHRY007	Galerucinae	?	12
6. CIXI002	Cixiidae	*Pintalia* sp.	12
7. ACHI002	Achilidae	*Plectoderes collaris* F.	11
8. CICA081	Cicadellinae	*Soosiulus interpolis* Young	11
9. DERB020	Derbidae	*Mysidia* sp.	10
10. DERB003	Derbidae	?	9
B. Felled trees			
1. ISSI002	Issidae	?	27
2. DERB008	Derbidae	*Herpis vittata* F.	15
3. TROP001	Tropiduchidae	?	11
4. PSYL003	Psyllidae	*Isogonoceraia* sp.	10
5. CIXI002	Cixiidae	*Pintalia* sp.	9
6. ACHI002	Achilidae	*Plectoderes collaris* F.	9
7. ACAN001	Acanaloniidae	?	9
8. CIXI006	Cixiidae	*Pintalia* sp.	8
9. DELP001	Delphacidae	?	8
10. ISSI009	Issidae	?	8
C. Understory			
1. PSYL003	Psyllidae	*Isogonoceraia* sp.	24
2. CHRY008	Eumolpinae	?	13
3. ACHI002	Achilidae	*Plectoderes collaris* F.	13
4. CHRY076G	Alticinae	?	13
5. CICA016	Coelidiinae	*Baluba parallela* Nielson	12
6. CIXI006	Cixiidae	*Pintalia* sp.	11
7. MEMB009	Membracidae	?	10
8. DERB022	Derbidae	?	9
9. ALEY006	Aleyrodidae	?	7
10. CICA028	Cicadellidae	?	7

in October (TABLE 1, compare adjusted data for felled trees). This paralleled the proportion of young foliage recorded in the samples: 3.7% on saplings in April > 3.3% on seedlings in April > 0.4% on seedlings in September > 0% on felled trees in October. Of 275 saplings surveyed, 134 did not harbor any herbivorous insects at all, and on only 21 saplings were there more than five herbivores present at the same time. These low densities, particularly of juvenile sap-sucking insects and leaf-chewing insects, were correlated with the presence of young foliage on the saplings ($r_s = 0.31$, $P < 0.001$ and $r_s = 0.24$, $P < 0.001$, respectively).

In terms of species richness, samples from felled *Eperua* trees were more speciose, as compared to *Eperua* seedlings (TABLE 1). The comparison with samples obtained from saplings was difficult, as numbers of individuals collected were very different. Unadjusted quantitative samples from felled *Eperua* trees suggest that these samples were more speciose than samples obtained from saplings (TABLE 1). An overlap of about 50% occurred in species composition between seedlings and saplings, a 30% overlap between saplings and felled trees, and a 15% overlap between seedlings and felled trees. Although suggesting that saplings were more similar to seedlings than to felled trees, this interpretation is not straightforward, because only a few individuals of most species were collected, and their preferences are therefore difficult to ascertain.

DISCUSSION

To consider what the insect samples obtained from the foliage of felled trees really represent, we discuss the problems related to tree felling and also the faunal differences between seedlings and parent trees.

TABLE 4. The 25 most common insect species collected from seedlings (Survey 11) and from the foliage of felled trees (adjusted data), compared Mann-Whitney tests ($N = 250$ samples).

Code	Identification	Seedlings	Felled trees	Mann-Whitney U
CIXI006	*Pintalia* sp.	100	8	38,842***
CICA004	*Soosiulus fabricii* Metcalf	81	1	69,508***
PSYL003	*Isogonoceraia* sp.	55	10	33,700**
ISSI002	?	0	27	34,250***
CIXI002	*Pintalia* sp.	12	9	30,888 n.s.
ACHI002	*Plectoderes collaris* F.	11	9	31,619 n.s.
CICA010	?*Oragua* sp.	15	4	32,502*
DERB008	*Herpis vittata* F.	3	15	32,750**
DERB020	*Mysidia* sp.	10	7	31,745 n.s.
CHRY007	?	12	3	31,999 n.s
CICA081	*Soosiulus interpolis* Young	11	0	32,625***
TROP001	?	0	11	32,625***
CIXI009	*Pintalia* sp.	7	3	31,750 n.s.
DELP001	?	2	8	32,000 n.s.
PLAT001	*Canopus* sp.	4	6	31,377 n.s.
ACAN001	?	0	9	32,250*
CICA080	?*Oragua* sp.	6	3	31,501 n.s.
DERB003	?	9	0	32,250*
ISSI009	?	1	8	32,000*
DERB007	*Mysidia* sp.	5	3	31,500 n.s.
FLAT014	Nr *Anormenis* sp.	0	8	32,250**
NOGO001	*Nogodina reticulata* F.	0	8	32,125**
DERB006	*Herpis* sp.	7	0	32,125**
DERB009	?	2	5	31,625 n.s.
TROP002	?	0	7	32,000*

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$; n.s., not significant.

Collection Problems Related to Tree Felling

The entomologist, when felling trees in rain forests to collect insect specimens from their foliage (e.g., Wilson 1959, Amedegnato 1997), is likely to face the following problems: a) insects may be disturbed and fly away during the felling process; b) falling trees may crash along with branches of surrounding trees, vines, and epiphytes, along with their insect associates; and c) understory insects not severely disturbed or injured by the impact may invade the foliage of felled trees within a short time (30 minutes in the present case).

The problem of insects flying away during the felling is impossible to evaluate with the present data but must be restricted to rather mobile insects. It may artificially depress insect densities on the foliage of felled trees. If this problem were considerable, it did not prevent higher densities on the foliage of felled trees than on that of seedlings. The significance of falling trees is also difficult to assess. It may have inflated figures for the species richness and insect density on the foliage of felled trees. Note that this problem also may occur when using methods such as canopy fogging and may be particularly serious when estimating insect host specificity from distributional records alone.

In our opinion, the problem of the invasion of felled trees by understory insects may be the most serious, considering the present data. It may have inflated the species richness and insect density on the foliage of felled trees. This is suggested by the similarity (and robustness of the analysis) between felled trees and understory samples (FIGURE 1). This problem is overshadowed, however, by the following factors: a) the more important dissimilarity of seedlings and felled trees samples (FIGURE 1); b) the often different taxonomic composition between the material collected on seedlings and felled trees, with notably more Cicadellinae on seedlings and more Fulgoroidea on felled trees (TABLE 2); c) poor correspondence in the ranking of species abundance among different datasets (TABLE 3); and d) strict preferences of common species for either seedlings or the foliage of felled trees (TABLE 4).

These data suggest that insects may be rather specific in their use of the forest strata, either specializing on the understory and seedling foliage or on the foliage of parent trees. Felling the trees, however, results in an influx of understory insects on the foliage of felled trees, and this may explain the higher similarity of samples from felled trees with understory samples than with seedling samples.

Amedegnato (1997) has studied arboreal grasshopper fauna extensively by felling large rain forest trees in the Amazon. She was even able to study the stratification of the insect species within tree crowns, stating that the insects appear to be rather undisturbed by the felling. Despite our scarce grasshopper data, it seems likely that small, very mobile insects may be more disturbed by the felling of trees than large grasshoppers. To avoid these problems, however, it may be safer to obtain samples from the foliage of trees in situ, rather than felling them. Our current project in Panama compares insect samples obtained in situ from saplings and parent trees.

Faunal Differences between Seedlings and Parent Trees

The various datasets examined suggest that parent trees support a more speciose insect fauna than conspecific seedlings. This issue may be complicated by the influx of species from the understory into the foliage of felled trees; but when understory species were removed totally from the data, the foliage of felled trees still supported more than twice the number of insect species of seedlings, for an equivalent sample size and sampling effort. Most likely these differences arise from differences in architecture between seedlings and parent trees (e.g., Lawton 1983). The effect of tree size per se, which may differ for various insect groups, may be particularly relevant to less mobile insects, such as caterpillars. Because of increased risks of starvation or predation on small plants, more caterpillars may be expected on the foliage of trees than on seedlings, unless they can move easily from one seedling to the other after defoliating them. Despite felled trees being devoid of young foliage, our data showed a higher abundance of caterpillars on trees than on seedlings.

For various reasons, insects may prefer foraging either in the understory or canopy. For example, very common species such as *Pintalia* sp. (CIXI006) and *Soosilius fabricii,* abundant in the shady understory, also were more common in small rather than large understory gaps (E. Charles unpubl. data). They appear to avoid sunny parts of the forest, and the few specimens found on the foliage of felled trees actually may originate from understory contamination. Sun-loving Membracidae species were rather abundant in the understory collections, particularly in large gaps (E. Charles et al. in prep.) but also on the foliage of felled trees. Membracids collected from felled trees and understory were, however, different species. The high incidence of Fulgoroidea, particularly Issidae, in samples obtained from felled trees appears consistent with what little is known about their vertical distribution in rain forests (e.g., Garrison & Willig 1996).

Seedlings also may appear to support more insect species than there really are. Most insects foraging on seedlings in Block 17 are rather generalists, and few resident insects appear to target seedlings as a food resource (Basset 1999). It is difficult to comment on insects foraging on parent tree foliage, since data about their host specificity are lacking.

Insect densities on the foliage of felled trees were often higher than on seedlings by a factor of 1.5 (3.2 against 2.1 individuals for a sample size of about 1.4 m^2), but these data are less convincing than for insect diversity. For example, in comparisons of seedlings, saplings, and felled *Eperua* trees, insect densities were not similarly higher on felled trees. All of these samples were dominated by the specialist psyllid, *Isogonoceraia* sp., whose nymphs feed on young foliage. Only five psyllid nymphs were collected from felled trees, whereas they represented about 30% of all insects collected on seedlings (Basset 1999). Many psyllid nymphs were collected from saplings, which included a relatively high proportion of young foliage. Unless sample size also refers to the area of young foliage surveyed, it may be difficult to relate differences in insect densities to host-plant architecture alone. We believe that if the felled trees had some young foliage, differences in insect species richness and densities between seedlings and parent trees would have been higher. The qualitative samples obtained from the foliage of felled trees, by greatly increasing the leaf area sampled, suggest that much larger areas of foliage examined would have increased considerably the differences between samples obtained from seedlings and from felled trees.

CONCLUSIONS

Despite methodological problems inherent in the felling of the trees and the small sample sizes available for analyses, the different insect datasets collected in Block 17 suggest that different insect species exploit the resources available in the understory and canopy. Few species were present both on seedlings and on the foliage of felled trees, and the species common in these samples were generalists also present in the understory collections (Basset 1999). Even for these species, it is not clear whether they may forage at different height in the forest or may have contaminated the foliage of felled trees from the understory.

In addition, our data suggest that the insect fauna of *Eperua* saplings and seedlings was more similar than that on felled *Eperua* trees. Thus many insect herbivores in Block 17 may be stratum-specific, either foraging in the understory or in the canopy. Understory insects, such as those foraging on seedlings, are often generalists, for instance, many species of xylem-feeding Cicadellinae (Basset 1999). A generalist classification is consistent with the low production of the understory compared to the canopy. A small resource base in the understory may not favor specialization of insect herbivores and species-rich communities (e.g., Price 1992, Basset 1996). Instead, a higher proportion of insect herbivores foraging in the canopy may be specialists than of those in the understory (Erwin 1983).

Comparing the study of Fowler (1985) on insects of seedling and parent birch trees in Britain with our Guyana study suggests that tropical rain forests may be much more heterogeneous for insect herbivores than are temperate forests. Host-plant effects may play a significant role in increasing the heterogeneity of tropical forests for insect herbivores (e.g., Janzen 1970), but illumination and other microclimatic factors, which differ considerably between the understory and the canopy, also may be important in this regard.

Our study has several obvious implications, providing that the conclusions are not obscured by methodological problems. First, the Janzen-Connell model is unlikely to be valid in the study system, because apparently very few insect species are being shared between seedlings and parent trees; and most insects foraging on the seedlings are generalists. Second, the host preferences of generalist insects in tropical rain forests, such as many species attacking seedlings in Block 17, may originate partly from foraging behaviors constrained by microclimate, illumination, or other requirements, that is, from the ability of generalists to tolerate different conditions in canopy vs. understory. Third, few insect species appear able to dominate both in the understory and canopy, perhaps with the exception of the psyllid *Isogonoceraia* sp. Last, understanding of possible vertical gradients in insect species richness in tropical rain forests should proceed with insect material collected in situ and with careful studies of host specificity and life history. For more information, a web site describing the project in Guyana can be found at (http://www.bishop.hawaii.org/bishop/natsci/guyana).

ACKNOWLEDGMENTS

Assistants who collected, mounted, and helped with the assignment of most of the insect material were Milton Allicock, Shawn Fiffee, Brentnal Hoyte, Henry James, Linsford La Goudou, Troy Lashley, Marlon Mclennan, Dayl Thompson, Terrence Washington, Martin Williams, and Orin Williams. Wilfred Jarvis, of the Guyana Forestry Commission, felled the parent trees in Block 17 with impressive skills. David Hammond, Raquel Thomas, Val Brown, and the Tropenbos-Guyana staff helped with various conceptual and logistical aspects of the project. Other much needed administrative and logistical help was provided by the Tropenbos-Guyana Programme, the International Institute of Entomology, the Overseas Development Administration, and Demerara Timbers Limited. Taxonomic help was provided by Hector Barrios, John Brown, Caroline Chaboo, Michael Cox, Mervin Nielson, Jacqueline Miller, Lois O'Brien, Eva Sprecher, and Mick Webb. Comments by Scott Miller and Neil Springate improved the manuscript. Work with Vojtech Novotny, Richard Pyle, and Scott Miller to develop an efficient method of data archival was possible through U.S. National Science Foundation grant DEB-97-07928. The various insect projects in Block 17 were supported financially by the Darwin Initiative for the Survival of the Species, British Airways (conservation travel scheme), the European Science Foundation (canopy program), the Overseas Development Administration (U.K.), and the Canadian International Development Agency.

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