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The effects of gap size and age on the understorey herb community of a tropical Mexican rain forest

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Summary

1. The effects of gap age and size on understorey herb communities and their light environments (indirect skylight and direct sunlight estimated from hemispherical canopy photographs) were investigated in a tropical rain forest in Los Tuxtlas, Veracruz, Mexico. Thirteen gaps, ranging in size from 70 to 700 m^2 and ranging in age from young (1–2 years old) to old ($\gg$5 years old), were studied.

2. The mean amounts of relative indirect skylight and relative direct sunlight were 0·083 and 0·116, respectively. Both kinds of light increased significantly with gap size and decreased significantly with gap age, but a significant interaction indicated that size was more important in new gaps than in intermediate-aged gaps.

3. Herbaceous communities were very diverse; 52 species were found in total. Most species occurred at low frequencies in most sites. The number of species per gap (mean = 15·2) was not affected significantly by gap age or size, although the Shannon–Weaver diversity index H' (mean = 2·1) was significantly highest in young gaps (mean = 2·4) followed by intermediate-aged gaps (mean = 2·1).

4. Total standing leaf area produced by herbs (mean = 0·795 $m^2 m^{-2}$) was significantly affected by both gap size and age; it was highest in intermediate-aged, medium-sized gaps (1·935 $m^2 m^{-2}$).

5. Hemiepiphytic aroids were numerically important at most sites. Terrestrial aroids and large monocots were also found to be important groups at many sites, not numerically, but by their relative contributions to total standing leaf area.

6. Species assemblages differed considerably between sites (mean proportional similarity, $PS = 40·8\%$). Intermediate-aged gaps were more similar to each other (mean $PS = 52·7\%$) than young gaps were to each other (mean $PS = 35·3\%$). Mature forest sites were the least similar to all the other sites (mean $PS = 28·9\%$).

7. Gaps of the same age and size were more similar in species assemblages than those that differed in size or age, but this trend was only of marginal significance.

8. There were reproductives at all sites; the highest relative number was in the intermediate-aged sites, not the bright sites, new gaps or young gaps.

10. The influence of gap size on the light environment is important in understanding the dynamics of the herbaceous communities. Gaps of intermediate age, the part of the forest that is in the 'building phase', are just as critical as the new-gap phase of the forest dynamics.

Key-words: aroids, cluster analysis, diversity, hemispherical canopy photographs, light

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Introduction

The effects of gaps on woody plants in tropical forests have received much attention (e.g. Denslow 1980, 1987; Bazzaz 1984; Brokaw 1985a,b; Martínez-Ramos 1985; Clark & Clark 1987) but relatively little is known about how gaps influence understorey herb communities in tropical forests (Smith 1987; Horvitz 1991). This study examines the influence of gap age and size on understorey herb communities and their light environments.

Several predictions were tested concerning the effects of gap age and size on the quantity of light in the understorey and on the diversity, density, leaf area and stage structure of the understorey herbaceous community.

1. The prediction that there is more light available to herbs in large and young gaps compared to smaller or older gaps was tested (Bazzaz & Pickett 1980; Augspurger 1984; Chazdon & Fetcher 1984; Clark 1986; Chazdon 1986; Smith 1987; Sanford, Braker & Hartshorn 1986).

2. Diversity, density and total standing leaf area of herbs were expected to be highest in young gaps and in large gaps, increasing with the size of the gap (cf. Brokaw 1985b) and decreasing over time (cf. Brokaw 1985a,b). This prediction is based on the idea that more species (both shade-intolerant and shade-tolerant) are able to live in large, young gaps because more light is available in such sites, while only shade-tolerant species can live in smaller or older gaps (Howe 1990a).

3. An analysis of proportional similarities between communities was made to investigate if gap age and size determined herbaceous species assemblages. If so, it was expected that communities from gaps of similar age and size would be more similar than those of differing ages or sizes, as has been hypothesized for woody plants (Denslow 1980, 1987; Martínez-Ramos 1985; Hubbell & Foster 1986). This prediction is based on the assumption that different species utilize gaps of different age or size classes so that the species assemblages of gaps of the same age or size class should be most similar (Denslow 1980, 1987; Orians 1982; Núñez-Farfán & Dirzo 1987; Brandani, Hartshorn & Orians 1988). If age or size class of gaps does not explain variation in species assemblages, diversification into niches may be less important than stochastic processes in rain-forest communities (see Hubbell & Foster 1986). There may also be significant niche heterogeneity within gaps as a function of proximity to gap edge (Howe 1990a,b), compass orientation (Poulson & Platt 1989) or position relative to the crown vs. the bole of the fallen tree (Núñez-Farfán & Dirzo 1987; Brandani *et al.* 1988), but this type of heterogeneity was not investigated in the current study.

4. The prediction that reproduction of understorey plants is restricted to the youngest or largest gaps (Smith 1987) was tested. This prediction is based on the idea that reproduction is energetically costly and that light is the limiting resource for reproduction.

Methods

Thirteen gaps of known ages (R. Dirzo, personal observation and S. Sinaca, personal communication) in three size classes were chosen at the Los Tuxtlas Field Station (18°34′N, 95°04′), State of Veracruz, south-eastern Mexico, in 1986 (five gaps) and 1988 (eight gaps), during the late rainy season (October) (Table 1). The vegetation at the Los Tuxtlas field station is classified as tall, tropical evergreen rain forest (Lot 1976; Dirzo 1987), a vegetation type characterized by canopy trees ⩾30 m tall. Each gap was measured by laying down two long metre tapes at right angles, one along its long axis and one along its short axis. The gap area was approximated by the area of the rectangle defined by these axes. These tapes established a grid coordinate system for each gap. Sites were chosen to represent gaps of three age classes (young, <2 years since gap formation;

Table 1. Understorey herb community and light environment characteristics for gaps of different ages and size in the tropical rain forest at the Los Tuxtlas Field Station, Veracruz, Mexico. There were ten 1-m^2 samples per site at all sites except at intermediate-aged large site 1, where there were only four samples. Indirect skylight (*ISF*) and direct sunlight (*DSF*) were measured relative to the amount of light in a completely open area, with only sky from horizon to horizon, by analysis of hemispherical canopy photographs (mean ± SD, $n = 10$)

Site	Age (years)	Size (m^2)	Density (no. m^{-2})	Total leaf area (m^2 m^{-2})	Diversity		Light	
					No. species	*H′*	*ISF*	*DSF*
Young (1–2 years)								
small 1	1	70·4	6·8	0·277	14	2·1	0·085 ± 0·049	0·089 ± 0·068
small 2	0·5	103·2	7·0	0·227	18	2·5		
medium 1	2	136·5	22·2	0·814	21	2·5	0·083 ± 0·047	0·127 ± 0·085
medium 2	1	148·4	14·0	1·290	16	2·3		
large	1	700	13·1	0·635	19	2·5	0·215 ± 0·049	0·353 ± 0·088
Intermediate (3–5 years)								
small 1	3	100	17·2	0·711	19	2·1	0·070 ± 0·025	0·110 ± 0·043
small 2	4	80·6	13·7	0·435	13	1·8	0·040 ± 0·018	0·046 ± 0·020
medium 1	3	204	6·0	2·087	10	1·9		
medium 2	3	136	16·4	1·782	13	2·0		
large 1	?	540	9·8	0·688	11	2·2		
large 2	4	448	19·4	0·842	22	2·4	0·064 ± 0·035	0·057 ± 0·033
Old (≫5 years)								
Old 1	≫5	400	16·2	0·351	9	1·5	0·027 ± 0·017	0·030 ± 0·021
Old 2	≫5	600	11·7	0·192	12	1·0		

intermediate, 3–5 years since gap formation; and old, ≫5 years since gap formation) and three size classes (small, <105 m^2; medium, 105–400 m^2; large, >400 m^2). For gaps of intermediate ages, the current size of the canopy opening was not of interest as the size criterion, but rather the size of the original canopy opening; this size was estimated in the field by extending the metre tapes beyond the current opening into the regrowth area as visually determined by examining the growth pattern in the canopy and on the ground. To represent oldest 'gaps', sites in mature forest that showed no evidence of a recent treefall were chosen and an arbitrarily large grid (400–600 m^2) was laid out, as the size of a previously occurring gap at these site was unknown.

At each site, ten 1-m^2 sample plots were chosen using pairs of random numbers to determine the location of each sample plot on the grid. A serious accident in 1988 (severe envenomation of R. Dirzo by *Bothrops asper* (fêr-de-lance)) made it impossible to complete the ten sample plots at one site and the data for that site are based on only four plots. In each plot, all the individuals of each herbaceous species on the forest floor were counted and measured. One very small shrub, *Schaueria calycobractea* — nomenclature for all the species mentioned in this paper follows Ibarra & Sinaca 1987 — was also included because it seems to be in the same guild as the herbs. A different method was used to estimate leaf area for plants rooted in the plots than for plants trailing across the plots. For each individual that was rooted in the plot, the major and minor diameters of its canopy (as viewed from above) were measured, while for each plant that trailed across the plot, the width and length of the space it occupied (approximated by a parallelogram) were measured. Plants were classified into four categories: trailing vines (plants that had trailing branches that grew across the plot but that did not originate in the plot), seedlings (plants that had recently germinated in the plot), intermediates (plants that were clearly older than seedlings, but not yet reproducing and that were rooted in the plot), and reproductives (plants that were flowering or fruiting and that were rooted in the plot).

For seven of the sites sampled in 1988, the quantity of light in each sample plot (ten per site, as above) was estimated with black-and-white hemispherical (fish-eye)-lens canopy photographs, using a Sigma Fisheye Lens (1:4, F = 8 mm) and CANOPY software (Rich 1990). Canopy-photograph estimates of light for understorey plants are highly correlated with measurements made by quantum sensors (Chazdon & Field 1987; Rich *et al.* in press). The camera was mounted on a self-levelling frame *c.* 1·5 m from the forest floor and orientated so that magnetic north would be at the top of the images. To calibrate the Sigma lens, a paper plate was photographed at various angles. The maximum angle of the lens was 70° and the lens was very nearly equiareal across all the angles (T. Herbert, C. Horvitz, R. Dirzo, A. Mendoza and G. Gómez, unpublished data). Given (i) the lens calibration data, (ii) the magnetic declination, estimated at 9°12′ (C. Johnson, personal communication), (iii) the latitude, 18°35′N (Lot 1976), and (iv) a properly orientated image, the program CANOPY estimates the relative amounts of direct sunlight (*DSF*) and indirect skylight (*ISF*) reaching plants that are growing in the spot where the image was taken (Rich 1990). *ISF* and *DSF* are reported relative to the amount of light that would be received by a plant living in a totally open habitat at the study site, with only open sky from horizon to horizon. The effects of gap age and size on ISF and DSF were analysed by two-way analysis of variance (SAS procedure GLM; SAS 1988).

For each gap, the following characteristics of the plant community were determined: density (number of individuals m^{-2}), total standing leaf area of herbs (m^2 of leaf area m^{-2}), number of species, and the Shannon–Weaver diversity index, H', where $H' = -\Sigma p_i \ln p_i$ and p_i is the relative abundance of species i in the community. To analyse the effects of gap age and size on these community characters, Friedman Block tests were performed as follows (see SAS 1988). To test for the effect of size, each community variable was ranked within each age class and an analysis of variance was performed on the effects of size on these ranks. Similarly, to test for the effect of age, each community variable was ranked within each size class and an analysis of variance was performed on the effects of age on these ranks.

The species assemblage at each site was characterized by a vector of the relative abundances of each species (number of individuals of species i/total number of individuals) and also by a vector of the relative leaf areas of each species (leaf area of species i/total leaf area of all species). The similarities of species assemblages between sites were analysed in a pairwise fashion with the proportional similarity index summed over all species, $PS = \Sigma \min.(p_{ai}, p_{bi})$, where p_{ai} is the relative abundance of species i in community a and p_{bi} is the relative abundance of species i in community b. This index varies from 0 (totally dissimilar assemblages) to 1 (identical assemblages). In this paper, the similarity index is reported as a percentage, $PS = PS \times 100$. Analysis of similarities between gaps also constitutes a measure of the patchiness, or diversity among gap communities: low average similarity indicates high diversity between sites (Brokaw & Scheiner 1989).

A cluster analysis (UPMGA, group average, unweighted pair-group method using arithmetic averages) (Krebs 1989) of the species assemblages was performed to obtain an understanding of the overall patterns of similarity among the 13 sites (SAS procedure CLUSTER with the 'Average Method' Option; SAS 1988). This analysis calculates the distance between a sample and an existing cluster as the arithmetic mean of distances between the sample and all the members of the cluster, as follows:

$$S_{J(K)} = [\Sigma(S_{JK})]/t_J t_K,$$

where $S_{J(K)}$ is the average distance between clusters J and K, S_{JK} the observed distances between each of the sites in J and K, and t_J and t_K are equal to the number of sites in clusters J and K, respectively. As a way of measuring distance, the program uses the root-mean-square of the Euclidean distance between sites, $[\Sigma(X_{ij} - X_{ik})^2]/n$, where X_{ij} and X_{ik} are equal to the number of individuals of species i in site j and the number of individuals of species i in site k, respectively and n is the number of species, to cluster the most similar sites together and then continues to group sites with clusters (or clusters with clusters) hierarchically, based on the similarity of the clusters with the sites (or with one another). A tree is then produced that visually summarizes the similarity relationships between all the sites.

To determine if age and size classification affected similarity, the pairwise *PS*s were classified into four groups depending upon whether the assemblages being compared were from gaps of the same age and size, different ages and different sizes, the same size but different ages, or the same age but different sizes. We tested if the classification of gaps by age or size differences had a significant effect on the degree of similarity among sites (SAS procedure NPARIWAY, Kruskal–Wallis test; SAS 1988).

The life-form structure of the communities was determined by grouping the plants into the following categories: monocotyledons, monocotyledonous vines, ferns, dicotyledons, dicotyledonous vines, dicotyledonous small shrubs, terrestrial aroids and hemiepiphytic aroids. For these categories, both the relative abundances and the relative leaf areas were examined for each gap-site.

Finally, the stage structure (the relative numbers of seedlings, intermediates and reproductives) of the herbaceous community in the gaps of different ages and sizes was examined. Only plants originating within the sample plots were included in this analysis; trailing vines were excluded.

Results

LIGHT

Relative indirect skylight (*ISF*) varied 34-fold, from 0·008 to 0·273 in the 70 1-m^2 plots (mean = 0·083, CV = 80·7); relative direct sunlight (*DSF*) varied 50-fold, from 0·009 to 0·450 (mean = 0·116, CV = 100·9, $n = 70$). ISF and DSF were highly positively correlated ($r = 0{\cdot}972$, $n = 70$, $P < 0{\cdot}0001$).

The quantity of light (both indirect skylight and direct sunlight) decreased significantly with gap age, comparing young to old (by 21% and 16% for *ISF* and *DSF*, respectively), and increased significantly with gap size, comparing small to large gaps (by 1·6-fold and 1·8-fold for *ISF* and *DSF*, respectively) (Table 2). However, medium-sized gaps did not differ significantly from large or small gaps in *ISF*, although they were significantly greater in *DSF* than small gaps (Table 2). The brightest site was the young, large gap, where *ISF* and *DSF* were 10 times greater than in the closed-canopy sites (Table 1). In the young gaps, the large site had 2–3 times more light than the small or medium-sized sites. In contrast, the difference between small and large gaps for the intermediate-aged sites was negligible (Table 1); this contrast indicates an interaction between gap age and size in their effects on light.

Thus, the quantity of light in the understorey, as measured both by *ISF* and *DSF*, was affected significantly by gap age and size and their interaction ($P < 0{\cdot}0001$, both analyses, all effects). Together, gap age and size and their interaction accounted for 71·4% of the variance in *ISF* and 75·3% of the variance in *DSF* between plots (for both *ISF* and *DSF*, d.f.$_{\text{model}}$ = 5 and d.f.$_{\text{error}}$ = 64; for *ISF*, error MS = 0·0014; for *DSF*, error MS = 0·0036.

Heterogeneity of light within gaps was quantified by examining the CV for *ISF* and *DSF* for each site. The lowest within-gap heterogeneity was found in the young, large site (CV = 23·0 and 24·9 for *ISF* and *DSF*, respectively). The highest within-gap heterogeneity was found in the old forest site (CV = 62·0 and 70·7 for *ISF* and *DSF*, respectively) and in the young, small gap (CV = 57·4 and 76·4 for *ISF* and *DSF*, respectively). The remaining gaps had intermediate heterogeneity in *ISF* (CVs ranging from 35·8 to 56·2) and in *DSF* (CVs ranging from 39·2 to 67·0).

Table 2. Light environments of understorey herbs in gaps of different ages and sizes in the tropical rain forest at the Los Tuxtlas Field Station, Veracruz, Mexico. Marginal means of *ISF* (indirect skylight) and *DSF* (direct sunlight) by age and size of gap. Both *ISF* and *DSF* are relative measures to the amount of light that would be found in a completely open pasture with only sky from horizon to horizon. Means followed by the same superscript letter within a column are not significantly different (Duncan's Multiple Range Test, $P < 0{\cdot}05$)

	ISF	*DSF*
Age		
young	0·127^a	0·190^a
intermediate	0·058^b	0·071^b
old	0·027^c	0·030^c
Size		
small	0·065^d	0·082^d
medium	0·083^e	0·127^e
large	0·102^e	0·146^e

COMMUNITY VARIABLES

Understorey communities were very diverse. There was a total of 52 species (Appendix), although a mean of only 15·2 species was found per site ($n = 13$, range 9–22) (Table 1). The number of species per site was not significantly affected by gap age or size (Table 3). By contrast, the diversity index H' (mean= 2·1, $n = 13$) did vary significantly with gap age (Table 3). Young gaps had the highest diversity (mean = 2·4, $n = 5$), followed by intermediate-aged (mean = 2·1, $n = 6$); the closed-canopy sites had the lowest understorey diversity (mean = 1·2) (see Table 1). Within the intermediate-aged sites, there was a weak trend toward increasing diversity with increasing gap size (Table 1).

Density (number of individuals per unit area) varied 3·7-fold between the sites (mean = 13·4, CV = 37·3, $n = 13$) (Table 1), but did not vary significantly with gap age or size. However, the total standing leaf area, which varied 10·9-fold between the sites (mean=0·795 $m^2 m^{-2}$, CV = 74·6, $n = 13$) (Table 1), did vary significantly both by gap age and size (Table 3). Generally, the intermediate-aged sites had the highest standing leaf area when compared with young sites of similar size or compared with old sites (Table 1). The maximum standing leaf area was found in the intermediate-aged, medium-sized sites (mean = 1·935 $m^2 m^{-2}$, $n = 2$). The lowest standing leaf area, which was an order of magnitude lower (0·192 $m^2 m^{-2}$), was in a closed-canopy site (Old 2, Table 1). The two young, small sites also had low leaf area, lower than the other closed-canopy site (Table 1).

Of the sites for which both light measurements and community variables were available, the site with the most light did not have the highest density, the highest total leaf area, or the largest number of species (Table 1). The diversity index, H', was highest at this site ($H' = 2·5$), but not exclusively; several other sites that had equally high H' did not receive nearly the same amount of light (Table 1). However, the site with the lowest light had the lowest H' ($H' = 1·5$) (Table 1).

Table 3. Friedman Block tests on the effects of gap age and size on the ranked diversity (number of species and H'), density, and total leaf area of the understorey herbaceous communities at 13 gaps in the tropical rain forest at the Los Tuxtlas Field Station, Veracruz, Mexico. For the test of the effects on age, $\text{d.f.}_{\text{model}} = 2$ and $\text{d.f.}_{\text{error}} = 10$. For the test of the effects of size, $\text{d.f.}_{\text{model}} = 2$ and $\text{d.f.}_{\text{error}} = 8$

	Age		Size	
Community variable	r^2	P	r^2	P
Diversity				
Number of species	0·210	NS	0·083	NS
H'	0·673	<0·01	0·475	<0·10
Density	0·105	NS	0·063	NS
Total leaf area m^{-2}	0·683	<0·01	0·760	<0·01

To determine if, on a finer spatial scale, the relative amounts of indirect skylight and direct sunlight (*ISF* and *DSF*) were correlated with density, standing leaf area or the number of species, these variables were calculated for each of the 70 1-m^2 samples for which there was also a hemispherical photographic image. Neither *ISF* nor *DSF* was significantly correlated with any of these variables calculated for the 1-m^2 plots. However, density was significantly positively correlated with number of species and with standing leaf area ($r = 0·60$, $P < 0·0001$, and $r = 0·39$, $P < 0·001$, respectively). Also, the number of species was significantly positively correlated with total leaf area ($r = 0·48$, $P < 0·0001$).

RELATIVE ABUNDANCES AND LEAF AREAS OF SPECIES

Most of the species occurred at low frequencies in most of the sites. Only 13 of the 52 species contributed ⩾10% of the individuals to a given site and there were only 1–5 such abundant species per site. Rarer species lumped together made up 20–50% of the individuals at a given site (Fig. 1a, Appendix).

Sites differed considerably in species composition and in patterns of relative abundance (Fig. 1a). Both of the closed-canopy sites were highly dominated by a single species, *Anthurium flexile*, constituting 50% and 79% of the individuals at these sites. None of the other sites was so dominated by a single species (Fig. 1a, Appendix). A few species were fairly abundant at several sites. For example, *Anthurium flexile* and *Monstera acuminata*, two hemiepiphytic aroids, were among the most abundant at eight of the 13 sites. Other species were abundant at only one site, for example the dwarf bamboo-like grass, *Cryptochloa strictiflora*, at site young–medium 1 (Fig. 1a, Appendix).

The relative leaf areas give a different picture of which are the most important species in the understorey community. For example, by the leaf-area criterion, *Anthurium flexile* was important at only two sites, the closed-canopy sites, and *Monstera acuminata* was important at six sites (Fig. 1b, Appendix). As in the relative numbers, most species contributed only a small proportion of the leaf area to the total of most sites. Only 16 of the 52 species contributed ⩾10% of the leaf area to a given site and there were only 2–5 such important species per site (Fig. 1b, Appendix). Of the 16 species, six were not among the 'most abundant species', as defined by the relative number of individuals. These species included very large monocot herbs, *Renealmia*, *Heliconia* and *Costus*, and an aroid with a life form that is very similar to these monocot herbs, *Spathiphyllum*. By

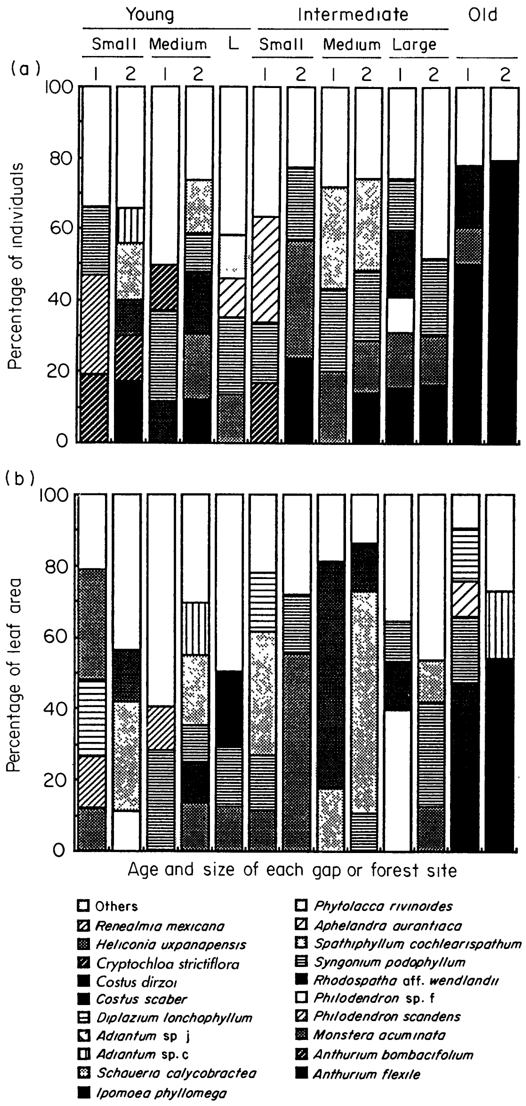

Fig. 1. (a) The relative abundances and (b) the relative leaf areas of the most abundant herbaceous species at each of 13 sites, including gaps and mature forest, in the tropical rain forest at the Los Tuxtlas Field Station, Veracruz, Mexico. Gap ages are classified as young, intermediate and old. Gap sizes are classified as small, medium and large (L). Only species representing ⩾10% of (a) the individuals or (b) the leaf area at a given site are distinguished. Rarer species are lumped together as others. Symbols used to represent species at each site are ordered vertically as in the legend.

the leaf-area criterion, the rarer species lumped together made up *c.* 8–40% of a given site.

The patterns of relative contributions to leaf areas varied between sites. None of the young gaps was dominated (⩾50% of leaf area) by a single species, while in three of the intermediate-aged gaps and one of the mature forest sites, a single species accounted for ⩾50% of the leaf area. *Monstera acuminata*, *Costus scaber* and *Schaueria calycobractea* were the dominants at these intermediate-aged gaps (contributing 55%, 63% and 62% to the leaf areas of their respective sites), while *Anthurium flexile* was the dominant at a mature forest site (contributing 54% to the leaf area).

RELATIVE ABUNDANCES AND LEAF AREAS OF LIFE FORMS

Hemiepiphytic aroids were numerically dominant in the understorey communities at most sites (Fig. 2a), with a mean (±SD) relative abundance of 68·8 ± 16·3%. At all sites >40% of the individuals were hemiepiphytic aroids, including five sites at which >75% were hemiepiphytic aroids. These aroids were also very important in terms of their contributions to leaf area at most sites (Fig. 2b), with a mean relative leaf area of 50·6 ± 24·7%. At

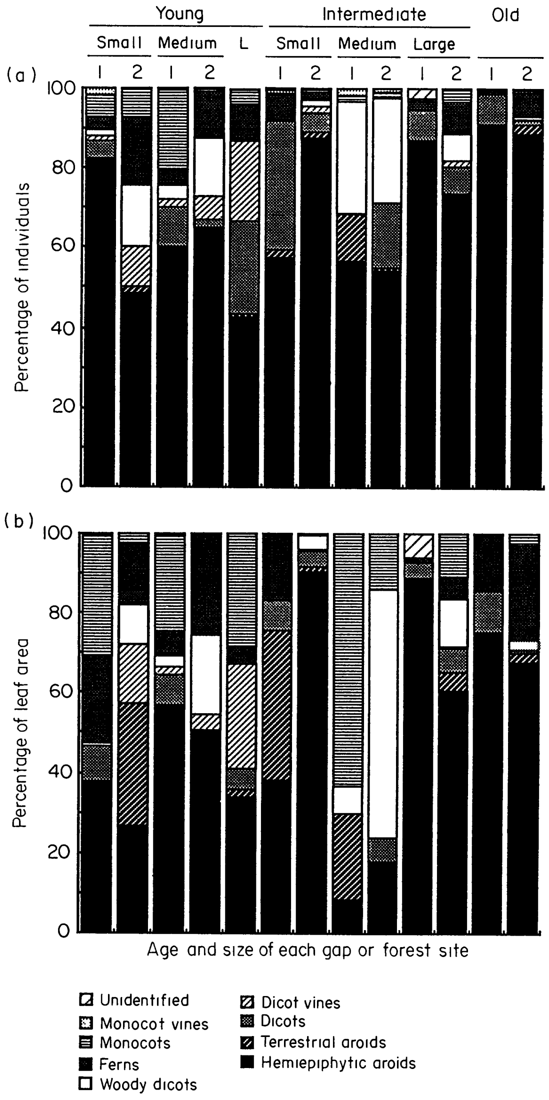

Fig. 2. (a) The relative abundances and (b) the relative leaf areas of major life-forms of the herbaceous species on the forest floor at each of 13 sites, including gaps and mature forest, in the tropical rain forest at the Los Tuxtlas Field Station, Veracruz, Mexico. Gap ages are classified as young, intermediate and old. Gap sizes are classified as small, medium and large (L). Symbols used to represent life-forms at each site are ordered vertically as in the legend.

seven sites, >40% of the leaf area was contributed by hemiepiphytic aroids, including three sites at which ⩾75% was contributed by them. Large monocots and terrestrial aroids were also important contributors to leaf area at many sites (Fig. 2b), with average relative contributions to standing leaf area of 13·7 ± 18·0% and 7·8 ± 12·7%. Monocots contributed ⩾25% of the leaf area at four sites, including one site at which 63% of the leaf area was contributed by them. Terrestrial aroids contributed >20% of the leaf area at three sites, including one at which they contributed 38% of the total leaf area.

PROPORTIONAL SIMILARITIES OF SPECIES ASSEMBLAGES

The species assemblages differed considerably between sites. On average, sites tended to have low proportional similarities to one another (mean = 40·8, CV = 34·3, $n = 78$ comparisons) (Table 4), a pattern that emphasizes the diversity of the understorey community on a larger spatial scale, i.e. its patchiness. The maximum similarity found was 68·9% (comparing the two intermediate-aged, medium-sized gaps) (Table 4). The other three *PS*s that were greater than 60% were for comparisons among intermediate-aged gaps (Table 4). Intermediate-aged gaps tended to be more similar to one another (mean = 52·7%, CV = 21·3, $n = 15$) than young sites were to one another (mean = 35·3%, CV = 26·1, $n = 10$). The minimum similarity was 7·7% (comparing a closed-canopy site to a young, large gap), which was the only comparison with less than 10% similarity. The closed-canopy sites were the least similar to other sites (mean = 28·9%, CV = 47·1, $n = 22$) (Table 4); of the six comparisons that had *PS* between 10% and 20%, five involved comparisons with closed-canopy sites.

The cluster analysis showed similar patterns to those described above. The tree of the distances between hierarchically defined clusters revealed three emergent patterns (Fig. 3). First, the highest similarity (smallest distance) was between and among intermediate-aged sites. Secondly, there was relatively low similarity (relatively greater distance) of the young-small gaps to (from) each other and between them and the other sites. Thirdly, the mature-forest sites formed a cluster that was very dissimilar (largest distance) from the cluster formed by combining all the other sites together.

Gaps of the same age and size were the most similar to one another (mean = 51·0%, CV = 29·3, $n = 6$) and gaps that differed in both size and age were the least similar to one another (mean = 37·1%, CV = 36·8, $n = 36$). Gaps of the same age but different size (mean = 44·7%, CV = 28·8, $n = 20$) and gaps of the same size but different ages (mean = 41·0%, CV = 35, $n = 16$ comparisons) were intermediate in similarity. This trend was in the expected direction, but classification of gaps by age or size differences was only of marginal significance in explaining the variation in *PS* values (Kruskal–Wallis test, $\chi^{2}{}_{3} = 6{\cdot}18$, $P = 0{\cdot}103$). If gap size and age were important determinants of understorey species assemblages we would expect a larger and significant difference among the means of these groups. The young, small sites were especially dissimilar (*PS* = 28·8%), lowering the average similarity of the same-age-and-size group. Thus, gap age and size did not account for the variability in the similarities among sites as much as expected.

Table 4. Proportional similarities of herbaceous communities in 13 sites, including gaps and mature forest, in the tropical rain forest at the Los Tuxtlas Field Station, Veracruz, Mexico

	Young sites (1–2 years)					Intermediate sites (3–5 years)						Old sites (≫5 years)	
	small 1	small 2	medium 1	medium 2	large	small 1	small 2	medium 1	medium 2	large 1	large 2	1	2
Young													
small 1		28·8	46·2	29·7	38·5	55·1	46·2	38·8	32·4	54·1	39·6	31·8	13·9
small 2			27·9	36·4	18·8	32·5	30·0	32·6	26·7	51·9	37·1	30·3	28·4
medium 1				42·1	49·0	50·0	48·9	48·9	40·8	57·7	54·5	40·3	12·7
medium 2					35·5	32·5	48·0	58·6	54·3	48·0	55·4	43·0	16·1
large						42·6	48·3	44·4	39·7	50·9	46·3	26·6	07·7
Intermediate													
small 1							45·5	46·8	34·6	59·3	49·7	39·5	20·2
small 2								58·3	34·6	66·0	54·9	49·1	30·3
medium 1									68·9	63·1	56·8	39·2	17·8
medium 2										50·6	37·4	19·6	11·0
large 1											63·7	47·9	27·5
large 2												57·5	24·9
Old													
old 1													57·3
old 2													

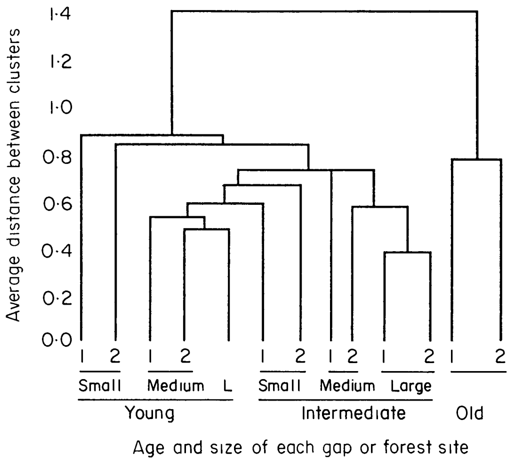

Fig. 3. Tree diagram for the cluster analysis of similarity of the herbaceous species assemblages of 13 sites, including gaps and mature forest, in the tropical rain forest at the Los Tuxtlas Field Station, Veracruz, Mexico. Gap ages are classified as young, intermediate and old. Gap sizes are classified as small, medium and large (L). Average distance (normalized root-mean-square distance according to the UPMGA, group average, unweighted pair-group method using arithmetic averages) between clusters is depicted and sites are hierarchichally clustered; the most similar sites have the smallest distance between them and occur on the same branches.

STAGE STRUCTURE

Reproduction in the understorey was not restricted to the youngest, largest gaps (Fig. 4). There were reproductives in all 13 sites (mean = 16·9%, CV = 94·1, $n = 13$) except one of the closed-canopy sites. The percentage of reproductives was generally highest in intermediate-aged sites (mean = 23·2%, CV = 90·0, $n = 6$); in particular, the maximum percentage of reproductives (60%) was in site intermediate–large 1. The youngest, large gap did not have an especially large proportion of reproductives (11·9%). The mean for the young sites was 14·8% (CV = 51·3, $n = 5$); in the young sites a medium-sized gap had the largest percentage of reproductives (27·4%). Mean *ISF* and *DSF* per site were not significantly correlated with the proportion of reproductives ($r_s = 0{\cdot}571$ and $r_s = 0{\cdot}464$, respectively; $n = 7$) or with the proportion of seedlings ($r_s = 0{\cdot}464$ and $r_s = 0{\cdot}214$, respectively; $n = 7$).

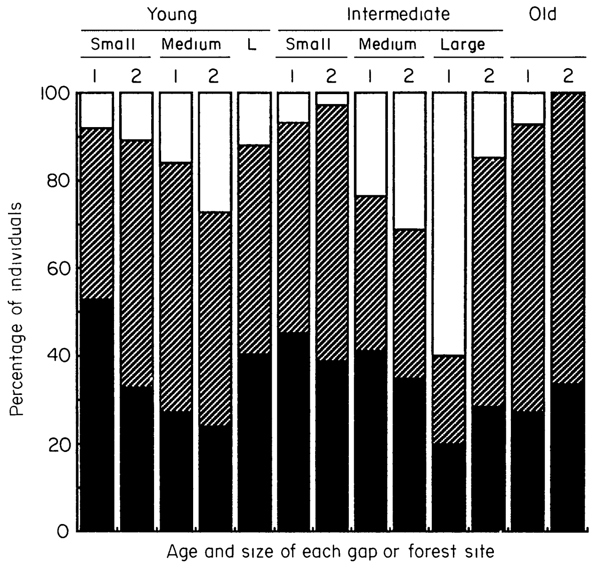

Fig. 4. The relative abundances of reproductives (□), intermediates (▨) and seedlings (■) at each of 13 sites, including gaps and mature forest, in the tropical rain forest at the Los Tuxtlas Field, Station, Veracruz, Mexico. Gap ages are classified as young, intermediate and old. Gap sizes are classified as small, medium and large (L). Only plants that were rooted in the sample plots were included; plants that only trailed across the plots were excluded from this analysis.

Discussion

The light environment of the sites did not vary entirely as expected. Although the quantity of light increased considerably with gap size in young gaps and was quite low in the closed-canopy sites, the expected trend of more light in the larger gaps was not found in the gaps of intermediate age. One possibility that we considered was that this may have been due to an unplanned bias in the sampling of gaps: whilst the young gaps varied in area 10-fold from small to large, the intermediate-aged gaps only varied fivefold in area. But even over this fivefold increase in original size of the gap, there was no trend of an increase in light. In fact, there was less light (as measured by *ISF* and *DSF*) in the 448-m^2 gap than in the 100-m^2 gap. To understand this result, it is important to bear in mind that the size of an intermediate-aged gap refers to the original size of the gap rather than its current size. In large young gaps, the additional light allows the surrounding vegetation to grow more quickly than in small young gaps, so that large gaps have a more rapid rate of closure than small gaps (see below). Heterogeneity of light in sample plots within the young, large gap was also low compared to other sites; in young, large gaps there is more light and more homogeneous light conditions. It is also quite likely that the geometry of gap closure differs between large and small gaps: large gaps closing from below and small ones from above or from the sides (Canham 1989; Howe 1990a; J. LeCorff, personal communication).

We compared our results with Howe's (1990b) study in which changing light levels of gap centres, gap edges and understorey were documented. He chose gaps ranging from 78 to 3142 m^2, with a mean of 611 m^2, so that the average gap of his study was equivalent in area to the large gaps of our study. He also estimated light environments with hemispherical canopy photographs that were digitized. The index used by Howe to measure light (% skylight) seems to be verbally similar to our index; however, it is quantitatively quite different. Whilst he reported an average value of 6·8% skylight for the gaps, we found values of 21·5% and 35·3% (for *ISF* and *DSF*, converted to percentages for ease of comparison) for gaps of comparable sizes. Quantitatively our values agree with those of other researchers utilizing the CANOPY program for analysing images (Rich *et al.* in press; C. Horvitz and J. LeCorff, personal observations). Nevertheless, a qualitative comparison can be made. Howe found no relationship between gap area and canopy openness. We found that gap size did have a significant effect on light, but that gap age and size interacted in their effects on light.

This may be relevant to another of Howe's findings. Over a 2-year period, gap centres declined in light-level by 43%, whilst gap edges declined in light levels by only 30%. Over the same 2-year period, the tree seedlings in gap centres increased in leaf area by 1800% as compared to the seedlings in gap edges that increased by only 690%. A comparable situation was reported for intra-gap variation in light-level dynamics and in growth dynamics of temperate forest gaps by Poulson & Platt (1989). In north-temperate-forest gaps, heterogeneity in light levels is determined by compass orientation rather than proximity to the centre of a gap. Northern edges receive 2·5 times more light than southern edges. Over a 13-year period, the northern edge of a gap declined in light level by 92% while the southern edge declined by only 50%, as the vegetation on the northern edge grew much more rapidly. These results emphasize that any initial heterogeneity in light levels within or between gaps will result in heterogeneous gap closure dynamics. This bears on our previous comment that large gaps may have more rapid rates of closure than small ones.

Of the community characteristics examined, most did not follow the expected patterns. Only diversity, as measured by H', showed the predicted trend of being highest in youngest and largest gaps, indicating that evenness is the component of diversity that was affected. Among the young gaps, however, H' was not affected by the size of the gap. Even though total leaf area varied significantly by gap age and size, as expected, the way it varied was unexpected. The highest total leaf area was in intermediate-aged rather than young gaps. Perhaps this is due to the past history of a site: an intermediate-aged site was a gap a few years ago and has had time to accumulate biomass, as compared to a new gap. The community characters, summarized by sample plot, were not correlated with the quantity of light in the sample plots.

We found a high diversity in the understorey community as a whole (52 species found in 13 sites, in 124 1-m^2 plots). Similar levels of diversity have been found in quantitatively comparable data sets by Smith (1987), who reported 65 species in 800 1-m^2 plots in Panama, and by Grubb *et al.* (1963), who found 58 species in 465 m^2 at a lowland site in Ecuador. High diversity in tropical forest understories has also been emphasized by Dodson & Gentry (1978), Gentry & Emmons (1987), A.W. Gentry (personal communication) and Poulsen & Balslev (1991). The numerical dominance of aroids reported in the present study has also been noted by Gentry & Emmons (1987). In contrast, the importance of leaf area of herbaceous monocots that we report for the understorey community has not been previously noted. The generality of these patterns should be investigated in additional tropical wet forests in future studies.

Our findings of low similarity between gaps and of the large number of rare species within most gaps further emphasize the diversity of the understorey herbaceous community. In the comparisons of the species assemblages across sites, we found that even the communities of like age and size were not very similar in species composition. This result indicates that stochastic processes as well as spatiotemporal heterogeneity in additional biotic factors (such as competition, predation, parasitism and pathogens) and abiotic factors (such as soil type and moisture) may contribute much to variation in the occurrence of understorey species. These factors may interact with the mosaic of environments created by treefalls and gap-phase regeneration. The similarity between the small, young gaps was especially low. This is intriguing, as it suggests that regeneration in small gaps is more heterogeneous than in large gaps. Analogous to the importance of drift for generating genetic diversity between small populations in population genetics, stochastic effects may be greatest in contributing to heterogeneity between small gaps. Simply because of size, each small gap samples a more restricted set of the available species.

We compared the results of our single-point-in-time census of the herbaceous communities in gaps of different sizes and ages to Brokaw & Scheiner's (1989) longitudinal study of woody communities in gaps. They studied 17 gaps that spanned the same range in sizes as ours (50–700 m^2) for 10 years. We found 52 species in 13 gaps, as compared to their 86 species in 17 gaps. They found 25–32% of the total species in any single gap; similarly, we found an average of 29% of the total in any single gap. They also analysed changes in density and diversity (measured by number of species) within gaps, and similarities among gaps over time (after 1, 5 and 10 years). Within-gap density and diversity were highest for intermediate-aged gaps, whilst between-gap similarity was lowest for young gaps and highest for intermediate-aged gaps. There were some parallels and some contrasts in our results. We found that there was no effect of age on density or on number of species, but that young gaps had the highest evenness, followed by intermediate gaps. We did find that intermediate-aged gaps had the highest leaf area. We also found intermediate-aged gaps to be more similar to one another than young gaps. These results underscore the importance of understanding the 'building phases' of gaps in tropical forest community dynamics for both herbaceous and woody plants.

The relative proportions of reproductives did not follow expectations. Instead of being highest in the youngest, largest gap, it was at a maximum in an intermediate-aged gap. Some of the plants that were reproductives were taller than the non-reproductives and higher than where we placed the camera to take the canopy images. Gap closure rate is partially a function of the height of the measurement (Lieberman, Lieberman & Peralta 1989; P. Rich, unpublished data; J. LeCorff, personal communication), so that, in a sense, the reproductives in the intermediate-aged gaps may still be in a fairly large gap by virtue of their height, even though our camera was not. It is interesting to note that total leaf area also peaked in the intermediate-aged sites. One potentially confounding factor is the phenology of reproduction and of seedling recruitment. Our data are for a single time and do not take into account that either reproduction or germination for many of the species may take place at a different time of year and have thus been missed by our single census. Nevertheless, our finding that reproduction is more prevalent in intermediate-aged gaps is consistent with the idea that fruiting resources for frugivorous animals are more abundant in the 'building phases' of gaps than in young gaps (Schupp *et al*. 1989).

In conclusion, the most salient aspects of our study are that; (i) the within-gap diversity and the between-gap diversity (or patchiness) of the herbaceous community was high; (ii) the differences in light environments of new gaps of different sizes caused differences in gap-closure dynamics that acted to make gaps of intermediate age more similar both in light levels and species composition to one another than young gaps were to one another; and (iii) the study of the intermediate-aged, or 'building-phase' gaps is critical for the understanding of tropical forest herbaceous community structure, composition and dynamics.

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Appendix. Relative abundance (%) and relative leaf area (in parentheses) of understorey plant species in (a) young (1–2 years old) and (b) intermediate-aged (3–5 years old) gaps of three size classes and in (c) mature forest sites in the tropical rain forest at the Los Tuxtlas Field Station, Veracruz, Mexico.

(a) Young sites

	Small		Medium		
Species	1	2	1	2	Large
Aroids (hemiephiphytic)					
Anthurium flexile	4·41 (0·89)	17·14 (6·60)	4·95 (1·33)	12·14 (4·50)	3·82 (1·83)
Anthurium crassinervum				0·71 (1·26)	
Anthurium bombacifolium	19·12 (2·56)	12·86 (4·35)	4·50 (1·53)		1·53 (0·62)
Anthurium sp. N			0·90 (0·22)		
Monstera acuminata	7·35 (12·25)		6·76 (7·47)	18·57 (13·56)	13·74 (12·85)
Philodendron saggitifolium			0·45 (0·14)	5·00 (8·82)	
Philodendron scandens	27·94 (14·43)	1·43 (0·45)	2·25 (2·06)	0·71 (0·39)	0·76 (1·09)
Philodendron sp. F		8·57 (11·43)			
Philodendron sp. M			2·70 (5·32)		
Rhodospatha wendlandii	2·94 (0·71)		11·71 (9·29)	17·14 (11·07)	
Syngonium podophyllum	19·12 (6·82)	2·86 (1·25)	25·23 (28·70)	10·71 (10·68)	21·37 (16·58)
Syngonium schottianum	1·47 (0·12)	5·71 (2·78)	0·90 (1·03)		1·53 (1·03)
Aroids (terrestrial)					
Diffenbachia seguine					0·76 (1·87)
Spathiphyllum cochlearispathum		1·43 (30·48)			
Dicots					
(Cucurbitaceae) sp. D				1·43 (0·19)	
Aphelandra aurantiaca	2·94 (8·68)		9·91 (7·28)		10·69 (3·71)
(Compositae) sp. E.				0·71 (0·31)	
(Compositae) sp. P.	1·47 (0·08)				
Phytolacca rivinoides					12·21 (1·60)
Dicot vines					
Indet. sp. R					4·58 (1·83)
Indet. sp. S					2·29 (0·20)
Indet. sp. T					3·82 (7·46)
Ipomoea phyllomega		10·00 (14·83)	1·80 (2·35)	4·29 (3·44)	6·11 (9·33)
Passiflora cookii	1·47 (0·07)			1·43 (0·35)	0·76 (0·72)
Passiflora sp. W					3·05 (6·53)
Woody dicots					
Schaueria calycobractea	1·47 (0·89)	15·71 (9·98)	3·60 (2·60)	15·00 (20·06)	
Ferns					
Adiantum sp. C				8·57 (14·06)	
Adiantum sp. J		10·00 (2·52)	1·35 (0·01)		
Asplenium sp. K		1·43 (0·54)			
Diplazium lonchophyllum	2·94 (21·68)	2·86 (8·89)	0·90 (5·70)	0·71 (5·82)	0·76 (0·04)
Indet. sp. B				2·14 (5·20)	
Indet. sp. H		1·43 (1·68)	1·35 (0·10)		
Indet. sp. U					8·40 (4·32)
Lygodium sp. I		1·43 (1·44)			
Monocots					
Heliconia latispatha		1·43 (0·11)			
Costus scaber			3·15 (1·84)		
Costus dirzoi		1·43 (0·65)	1·35 (1·88)	0·71 (0·29)	3·05 (21·02)
Cryptochloa strictiflora			12·61 (8·91)		
Heliconia uxpanapensis	5·88 (30·47)	1·43 (0·11)			
(Commelinanceae) Indet. sp. V					0·76 (7·38)
Renealmia mexicana		2·86 (1·91)	3·15 (11·92)		
Monocot vines					
Dioscorea sanosticta	1·47 (0·34)				
Indet.					
Indet. sp. L			0·45 (0·31)		
Totals					
Number of individuals	68	70	222	140	131
Leaf area (m^2)	(2.774)	(2.277)	(8·140)	(12·903)	(6·353)

(b) Intermediate-aged sites

	Small		Medium		Large	
Species	1	2	1	2	1	2
Aroids (hemiepiphytic)						
Anthurium flexile	9·88 (2·69)	24·09 (10·29)	6·67 (0·15)	14·02 (1·76)	15·38 (6·47)	16·49 (3·85)
Anthurium bombacifolium	16·86 (3·90)	1·46 (0·40)			5·13 (0·61)	9·79 (5·96)
Indet. sp. A	—		3·33 (0·22)			
Monstera acuminata	6·98 (11·46)	32·85 (55·41)	20·00 (4·51)	14·63 (4·36)	15·38 (9·88)	13·40 (12·48)
Philodendron saggitifolium	1·16 (0·89)		3·33 (0·04)			
Philodendron scandens	1·16 (1·27)	6·57 (4·90)				2·06 (3·04)
Philodendron sp. F	1·16 (0·50)				10·26 (39·93)	1·03 (0·23)
Philodendron sp. M	0·58 (0·02)				2·56 (3·40)	0·52 (0·26)
Rhodospatha wendlandii	2·33 (1·30)	2·19 (2·75)		6·10 (0·94)	17·95 (13·15)	1·55 (1·08)
Syngonium podophyllum	16·86 (15·69)	20·44 (16·61)	23·33 (3·29)	19·51 (10·67)	15·38 (11·49)	21·65 (29·39)
Syngonium schottianum	0·58 (0·35)				5·13 (3·78)	6·70 (4·37)
Aroid (terrestrial)						
Diffenbachia seguina	0·58 (3·27)	1·46 (1·43)	6·67 (3·59)	0·61 (0·17)		0·52 (4·86)
Spathiphyllum cochlearispathum	1·16 (34·47)		5·00 (17·99)			
Dicots						
Aphelandra aurantiaca	29·65 (6·72)	5·11 (3·79)		6·71 (1·30)	7·69 (4·00)	6·19 (5·30)
(Cucurbitaceae) Indet. sp. D						0·52 (0·49)
Lippia myriocephala				1·22 (0·26)		
Odontonema callistachyum	2·91 (0·66)			7·93 (3·95)		
Pavonia schiedeana				0·61 (0·38)		
Dicot vines						
Indet. sp. O					0·52 (0·19)	
Ipomoea phyllomega		1·46 (0·46)			1·03 (0·28)	
Woody dicots						
Schaueria calycobractea		1·46 (3·67)	28·33 (6·69)	26·22 (62·21)		6·70 (12·00)
Ferns						
Asplenium sp. K						2·58 (0·12)
Diplazium lonchophyllum	6·40 (16·30)	0·73 (0·05)				3·61 (4·46)
Indet. sp. B						0·52 (0·06)
Indet. sp. G		1·46 (0·05)				1·03 (0·77)
Indet. sp. U					2·56 (1·18)	
Lygodium sp. I						0·52 (0·02)
Monocots						
Calathea microcephala				0·61 (0·20)		
Costus scaber	0·58 (0·28)	0·73 (0·21)	1·67 (63·47)	1·22 (13·75)		2·06 (4·06)
Heliconia uxpanapensis						1·03 (6·71)
Monocot vines						
Dioscorea floribunda	0·58		1·67 (0·05)			
Dioscorea sanosticta				0·61 (0·02)		
Indet.						
Indet. sp. L	0·58 (0·23)					
Indet. sp. X					2·56 (6·10)	
Total						
Number of individuals	172	127	60	164	39	194
Leaf area (m^2)	(7·109)	(4·351)	(2·087)	(17·820)	(2·753)	(8·424)

(c) Old sites

Species	Old 1	Old 2
Aroids (hemiepiphytic)		
Anthurium flexile	50·00 (23·39)	79·31 (54·06)
Anthurium bombacifolium	8·02 (2·94)	4·31 (3·42)
Monstera acuminata	10·49 (18·67)	0·86 (0·23)
Philodendron scandens	3·09 (3·11)	
Philodendron sp. F		3·45 (3·59)
Rhodospatha wendlandii	17·28 (23·74)	0·86 (6·40)
Syngonium podophyllum	1·85 (3·30)	
Aroids (terrestrial)		
Diffenbachia seguina		2·59 (2·59)
Spathiphyllum cochlearispathum	0·62 (0·00)	
Dicots		
Aphelandra aurantiaca	7·41 (10·13)	
(Cucurbitaceae) Indet. sp. D		0·86 (0·56)
Woody dicots		
Schaueria calycobractea		0·86 (2·35)
Ferns		
Diplazium lonchophyllum	1·23 (14·72)	2·59 (18·73)
Indet. sp. G		
Monocots		
Calathea microcephala		0·86 (2·87)
Total		
Number of individuals	162	117
Leaf area (m^2)	(3·509)	(1·916)